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Molluscan Research

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- Headings for all taxonomic categories in taxonomic papers should be centred.
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Examples of format for species synonymy:

Xus yus Smith, 1902: 304, pl. 3, fig. 4A; Jones, 1934: 456; Dick, 1956: 23, pl. 2, fig. 6. [Example of an available name.]

Wus yus (Smith, 1902). Gail, 1978: 56, pl. 4, fig. 5. [Example where genus name has been changed.]
Xus mus. – Hope, 1987: 21, pl. 3, fig. 8; Fred, 2000: 400 (not of Black, 1934). [Example of misidentification.]

Example of format for genus synonymy:

Xus Smith, 1902: 303. Type species (by subsequent designation of Jones, 1934: 456): *Xus yus* Smith, 1902; Recent, Bolivia.

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 - The ‘telegraphic’ style is required for both.
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References

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Place a comma and a single space between the author's surname and first initial and one space between the initials (e.g. Smith, E. A.).

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Microscopic structure of the mantle and palps in the freshwater mussels *Velesunio ambiguus* and *Hyridella depressa* (Bivalvia : Hyriidae)

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Abstract

There has been increasing interest in freshwater mussels (order Unionoida) in recent years because their numbers are declining in many parts of the world and also because they have potential as monitors of pollution. Most studies have been performed on the families Unionidae and Margaritiferidae from North America and Europe, and comparatively little is known of the Hyriidae from Australasia. The present study describes the microscopic structure of tissues in the mantle and palps of two hyriid mussels, namely *Velesunio ambiguus* and *Hyridella depressa*, as viewed by light and electron microscopy. The two mussels show similarities with the unionids and margaritiferids, particularly the presence of extracellular mineralised granules. The mantle and palps of *V. ambiguus* and *H. depressa* consist of flaps of tissue bordered on the inner and outer surfaces by simple epithelia. The intervening tissue is dominated by connective tissue containing vesicular cells, muscle, nerves and blood spaces with haemocytes. Orange–yellow extracellular calcified granules are a prominent feature of the interstitial tissues. The abundance of calcified granules in the mantle of *H. depressa* is greater than that in *V. ambiguus* and there are differences in the appearance of the apical vesicles in epithelial cells.

Additional keywords: Australia, connective tissue, epithelium, granules, ultrastructure.

Introduction

The Australian freshwater mussels *Velesunio ambiguus* (Philippi, 1847) and *Hyridella depressa* (Lamarck, 1819) belong to the family Hyriidae, order Unionoida (Smith 1996; Walker *et al.* 2001). The Hyriidae is generally included in the superfamily Unionoidea (which includes the Hyriidae, Margaritiferidae and Unionidae), although recent studies suggest that it should be assigned to the superfamily Etherioidea (Graf 2000; Walker *et al.* 2001).

Recently, there has been increasing interest in freshwater mussels because populations have shown major declines in many parts of the world, including parts of Australia (Byrne 1998; Walker *et al.* 2001) and basic knowledge is required to develop appropriate conservation strategies. Studies of ultrastructure can also reveal effects of pollutants and environmental stress (Seiler and Morse 1988; Triebeskorn *et al.* 1991).

Whereas the ultrastructure of the unionids and margaritiferids has been examined in a number of papers, there have been few studies on the hyriids. Most studies have concentrated on the structure and composition of the extracellular granules because these granules can accumulate pollutant metals and, therefore, are of interest in pollution studies (Jeffree and Simpson 1984; Adams *et al.* 1997; Adams and Shorey 1998; Vesk and Byrne 1999; Byrne 2000). The present study makes a more general examination of the tissues of the mantle and palps by light microscopy (LM) and electron microscopy (EM).

Materials and methods

Specimens of *Velesunio ambiguus* and *Hyridella depressa* were collected from the banks of the Nepean River near the town of Menangle, NSW, Australia.

Mussels were opened by cutting the adductor muscles with a scalpel and the palps and pieces of mantle (approximately 5×10 mm) were dissected. For scanning EM (SEM), the tissue was placed into a modified Karnovsky fixative (3% formaldehyde, 2% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.4) for 24 h (Jeffree and Simpson 1984). Tissues were then washed in 0.1 M cacodylate buffer, dehydrated and critical-point dried. Pieces of tissue were mounted on SEM stubs, sputter coated with gold and examined in a Jeol JSM T-20 scanning electron microscope.

For transmission electron microscopy (TEM) and LM, small pieces (approximately 2 mm²) of palp and mantle tissue were placed in fixative. Two fixatives were used: either 3% formaldehyde, 2% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.4 (cacodylate-buffered fixative; CBF) for 24 h or 3% glutaraldehyde in 0.02 M HEPES buffer, pH 7.2 (HEPES-buffered fixative; HBF) for 1 h. The latter method is preferred for freshwater organisms because of the low osmotic potential of the buffer. Tissues were post-fixed with 0.1 M osmium tetroxide buffered with cacodylate or HEPES according to the fixative used, washed and dehydrated in an ethanol series, then infiltrated with propylene oxide and embedded in Spurr's resin. Sections were stained with uranyl acetate and lead citrate and examined in a Jeol 100S transmission electron microscope.

For LM, semithin resin sections (0.5 µm) were stained with toluidine blue or with methylene blue—Azure II—Basic Fuchsin (Hayat 1989).

Results

General anatomy

The macroscopic anatomy of *Velesunio ambiguus* and *Hyridella depressa* was similar to the better-known unionid mussels (Pearse *et al.* 1987). The two mantle lobes lined the inner surfaces of the shell and were elaborated at the posterior end to form pigmented inhalant and exhalant siphons. The mantle and palp tissues showed varying amounts of cream–orange pigmentation that was associated with mineralised granules. *Hyridella depressa* showed marked orange pigmentation in the palps and the mantle central zone (the region within the pallial line; terminology after Bubel (1973)) and margins. *Velesunio ambiguus* showed orange pigmentation in the palps, gills and along the mantle margin, but the central zone of the mantle was generally translucent, except for a cream or yellow patch towards the posterior in some specimens.

In LM sections, the central zone of the mantle in both species (Fig. 1a,c) consists of a sheet of tissue with thin outer and inner epithelia separated by a loose interstitial tissue containing haemolymph spaces, haemocytes, muscles, nerves and variable numbers of large vesicular cells (Fig. 1a,b,c). The two species differed in the appearance of the interstitial tissue. In the central zone of the mantle of *V. ambiguus* (Fig. 1a), there were generally loosely packed vesicular cells and large extracellular spaces, often traversed by thin muscle fibres. Clumps of calcified granules were rare, except in the patch towards the posterior of the animal. In *H. depressa* (Fig. 1c,d), the interstitial tissue was similar to *V. ambiguus* in Fig. 1a, but with numerous clusters of granules among the vesicular cells. In some *H. depressa* specimens, the tissue was much denser, as shown in Fig. 1c. Larger granules were also often found scattered through the tissue. Near the mantle margin in both species, the tissue became more densely packed with muscles, clusters of granules, vesicular cells and collagen fibres and the extracellular spaces were smaller.

The distal edge of the mantle margin was thickened and formed into three major folds (Fig. 1b), which are generally considered to be secretory (outer fold), sensory (middle fold) and muscular (inner fold) (Morse and Zardus 1997); the periostracum emerged from the groove between the outer and middle folds. The outer fold was often further divided into

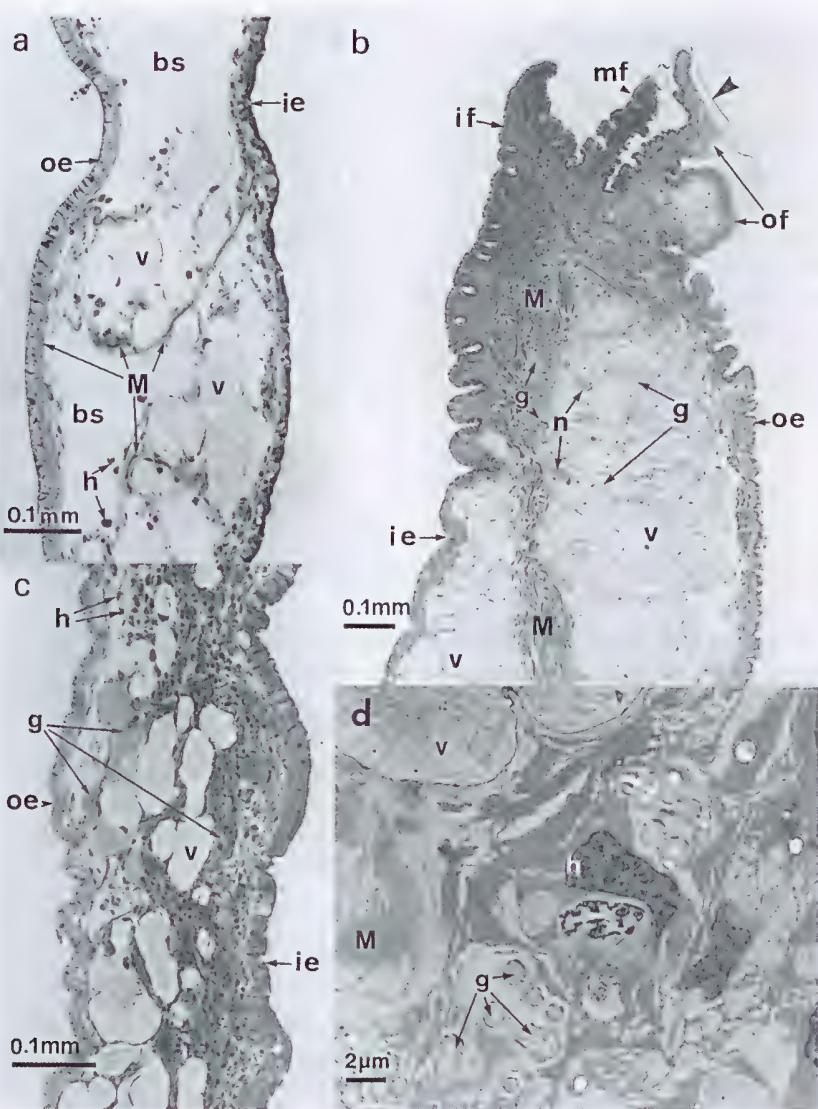


Fig. 1. Mantle. (a) *Velesunio ambiguus* mantle, central zone (HEPES-buffered fixation (HBF), toluidine (tol.) blue, light microscopy (LM)). The outer and inner epithelia (oe and ie, respectively) enclose loosely packed interstitial tissue containing blood spaces (bs), haemocytes (h) and vesicular cells (v). Thin bands of muscle (M) traverse the mantle and lie against the epithelial layers. (b) *Velesunio ambiguus* mantle margin, radial section (cacodylate-buffered fixation (CBF), tol. blue, LM). The edge of the mantle forms three main folds (if, inner fold; mf, middle fold; of, outer fold), with the periostracum emerging between the middle and outer folds (arrowhead). The tissue is more densely packed than in the central zone. M, Muscle; v, vesicular cells; n, nerve bundles; g, clusters of granules. (c) *Hyridella depressa* mantle, central zone (HBF, tol. blue, LM). Example of a mantle with densely packed interstitial tissues. oe, Outer epithelium; ie, inner epithelium; g, granules; h, haemocytes; v, vesicular cells. (d) *Hyridella depressa* mantle, central zone, montage of interstitial tissue (CBF, transmission electron microscopy). A vesicular cell (v) with a mass of storage material and thin peripheral cytoplasm is visible at the top left of the picture. A large haemocyte (h) contains several lysosomes. Laminar extracellular granules (g) lie scattered among the filamentous processes from haemocytes and muscle cells (M).

two or more lobes; examination of a series of previously prepared wax sections showed two or three lobes in nine of 10 *H. depressa* and four of 10 *V. ambiguus* (A. E. Colville, personal observation). The edge of the mantle margin was crossed by several bands of dense muscle. The largest of these ran from the inner surface at the base of the inner fold across to the pallial line. Muscle fibres also ran across from the base of the inner fold to the base of the outer fold. Between the muscle bands, there were clusters of vesicular cells and usually several clumps of calcified granules (Fig. 1b).

The oral (apposed) surfaces of each pair of labial palps were deeply ridged and densely ciliated (Fig. 2a–c). The ridges led down to the ciliated oral groove. The outer surfaces were comparatively smooth with scattered patches of cilia, although, towards the anterior, there were irregular protuberances (Fig. 2d,e).

The interstitial tissue in the palps was also dominated by vesicular cells and muscle (Fig. 2b,c). Clusters of granules occurred in both species, sometimes in large quantities (Fig. 2b,c).

Interstitial tissues

Vesicular cells

The vesicular cells (Figs 1a,b, 3) were large, with a central region filled with fine granular storage material and a thin peripheral layer of cytoplasm containing the nucleus. Near the nucleus, the cytoplasmic layer was thicker and contained many vesicles of varying electron density (Fig. 3). Fine cytoplasmic extensions often projected from the cell surface.

Nerves and glio-interstitial cells

Nerve trunks in the mantle and palp contained a number of axons of different sizes and usually some glio-interstitial cells containing large, electron-dense granules (Fig. 4a). Some axons contained neurotubules approximately 20–25 nm in diameter. Nerves containing small dense-core vesicles were common in large nerve trunks and in the finer subepithelial tracts. Electron-lucent vesicles were less common. The two types were sometimes mixed within one fibre. Specialisations of the nerve membranes were occasionally observed, presumably representing synaptic connections (Fig. 4b–d). The glio-interstitial cells usually lay on the periphery of the bundle, but did not form sheaths around the axons (Fig. 4a,b,d). Both glio-interstitial cells and nerves formed connections with the lateral processes on muscle cells. Glio-muscle connections were particularly prominent on the lateral projections from muscle cells in arterial walls (Fig. 4e).

Muscle

Muscle cells contained thick and thin filaments and dense bodies (Fig. 5a,b,d), with no cross striations. Mitochondria lay peripherally, often in large lateral cytoplasmic projections. When fixed with CBF, the lateral projections often contained large amounts of granular material that resembled glycogen rosettes (not shown). With HBF, this material usually appeared to be leached out (Fig. 5d, spaces in lateral projections).

Muscle cells varied in size, from large thick cells (up to 8 µm in diameter) in the muscle bands traversing the distal margin of the mantle to thin fibres (1–2 µm in diameter) lying under the epithelia and associated with nerve tracts. The thick fibres (Fig. 5a) generally had short lateral processes with subsarcolemmal cisternae and few visible mitochondria. Thinner fibres, such as those traversing the mantle (Fig. 5b) or forming the walls of arteries (Fig. 5c,d), often had many lateral processes containing mitochondria. The lateral processes

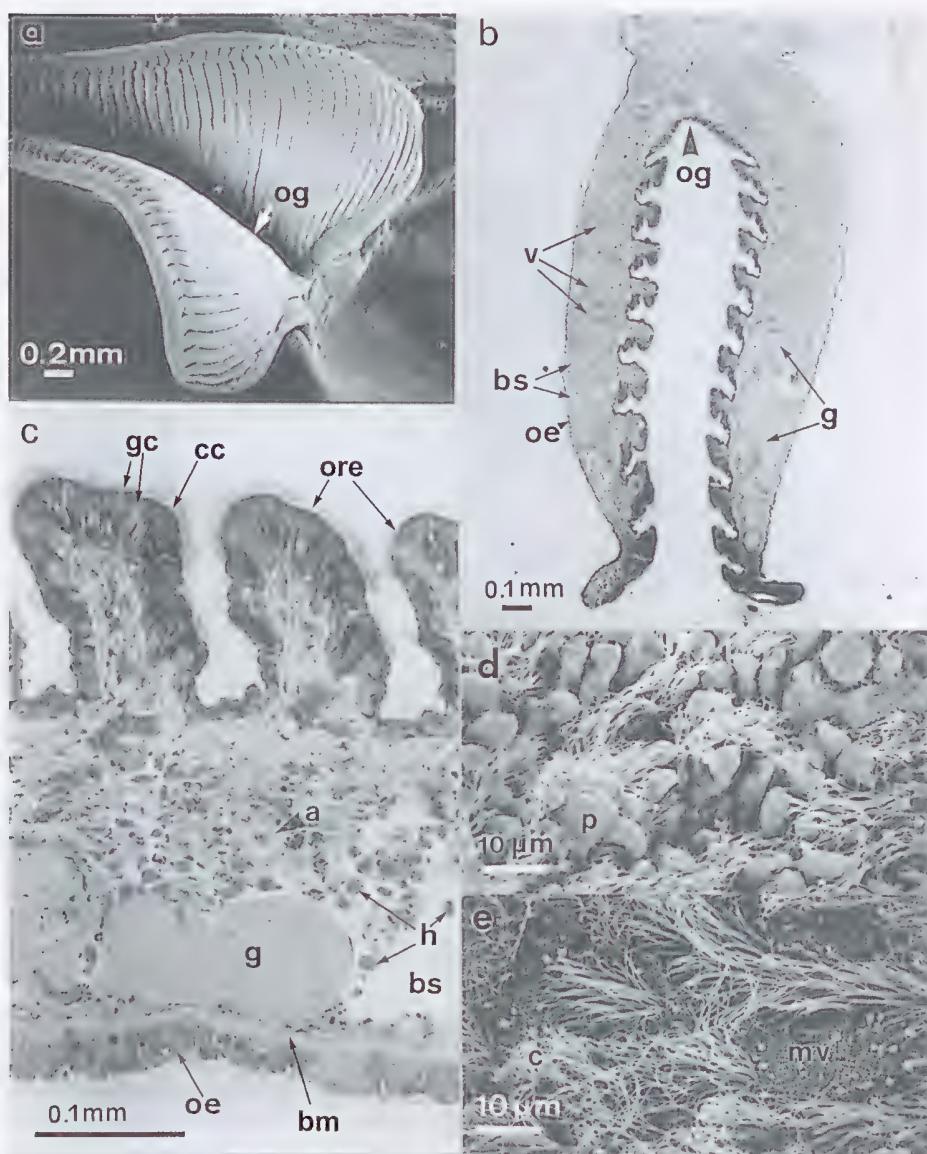


Fig. 2. Labial palps: general anatomy. (a) *Velesunio ambiguus* labial palps (scanning electron microscopy (SEM)). Ridges in the oral epithelium lead down to the oral groove (og). (b) *Hyridella depressa* labial palps, oblique section (cacodylate-buffered fixation (CBF), toluidine (tol.) blue, light microscopy (LM)). The interstitial tissue is packed with clusters of granules (g), interspersed with a few vesicular cells (v) and blood spaces (bs). Ridges of the inner (oral) epithelium are covered with columnar ciliated cells and some glandular cells. (c) *Velesunio ambiguus* labial palp (CBF, tol. blue, LM). Columnar ciliated cells (cc) and glandular cells (gc) cover the ridged oral epithelium (ore). The cells of the outer epithelium (oe) are shorter and rest on a thick basement membrane (bm). In the interstitial tissue, large clusters of granules (g), haemocytes (h), blood spaces (bs) and a small artery (a) can be identified. (d,e) *Hyridella depressa* labial palps (SEM). The outer surface shows considerable variation in the surface structure. (d) The surface is irregular with protrusions (p); (e) the surface is relatively smooth and covered with microvilli (mv) and clumps of cilia (c).

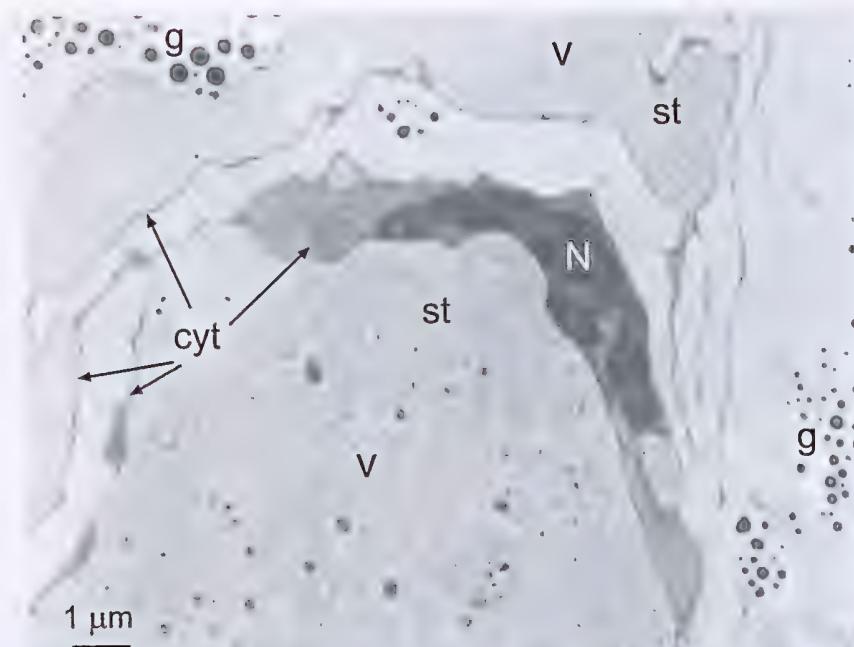


Fig. 3. Vesicular cells. *Velesunio ambiguus* mantle margin (cacodylate-buffered fixation, transmission electron microscopy). Vesicular cells contain a mass of fine granular stored material (st), covered by a thin superficial layer of cytoplasm (cyt) that extends into filamentous projections. The cytoplasm near the nucleus contains vesicles of secretory material. Small electron-dense granules (g) are scattered in the extracellular matrix.

of the muscles in the artery walls made contact with many glio-interstitial cells and nerve endings (Fig. 5c,d). Myomuscular junctions were generally convoluted, but did not appear to involve any membrane specialisation.

Haemocytes

The most common type of haemocyte observed in these mussels was a large granulocyte with vesicles 1–2 μm in diameter, containing amorphous material. (These vesicles would commonly be termed 'granules' in descriptions of haemocytes because of their granular appearance by LM. However, in this description they will be termed 'vesicles' to avoid confusion with the electron-dense 'granules' described below.) In semithin sections, these vesicles stained blue with toluidine blue or bright turquoise with methylene blue–Azure II–Basic Fuchsin (Figs 1a,b, 2c). Using TEM, large medium-density vesicles were visible (Figs 6a,b, 7b). The appearance of other organelles varied slightly, depending on the fixative used. With 0.02 M HBF, large numbers of small electron-lucent tubules were present (Fig. 6a), whereas in 0.1 M CBF they appeared much less distended (possibly because of the higher osmotic potential of the buffer) and contrast was poorer (Fig. 6b). These cells also contained small amounts of endoplasmic reticulum, glycogen, scattered mitochondria and, occasionally, a Golgi body.

There were also smaller numbers of haemocytes without large vesicles. These had variable nucleus/cytoplasm ratios and variable numbers (from none to many) of small 0.2 μm -diameter medium-density vesicles (Figs 6c,d, 7b). Strands of rough endoplasmic

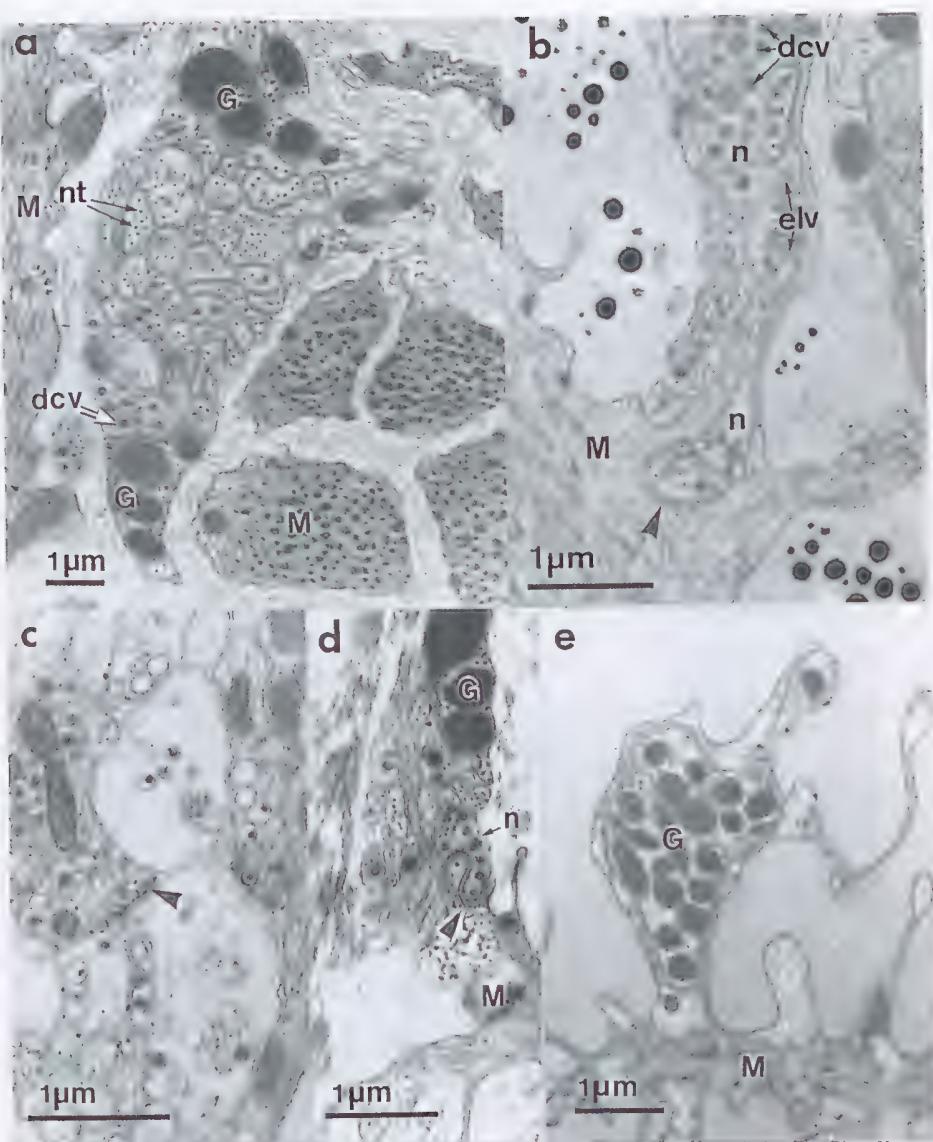


Fig. 4. Nerve and muscle. (a) *Hyridella depressa* mantle margin (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). A transverse section through a nerve bundle shows a range of axon profiles, neurotubules (nt) and small dense-core vesicles (dcv). Glio-interstitial cells with large electron-dense vesicles (G) lie on the periphery, but do not enclose the fibre. Muscle cells (M) are seen in cross-section (right) and oblique section (left). (b) *Velesunio ambiguus* mantle (HBF, TEM). A neuromuscular connection with membrane specialisation and post-synaptic cisterna is shown (arrowhead). The nerves (n) contain dense-cored vesicles (dcv) and small electron-lucent vesicles (elv). (c) *Hyridella depressa* palp (HBF, TEM). A putative synapse in a nerve trunk is shown (arrowhead). The presynaptic membrane shows increased density and small electron-lucent vesicles are accumulated along the membrane. (d) *Hyridella depressa* mantle central zone (HBF, TEM). A connection between a nerve (n) and muscle (M), showing increased density of the membrane (arrowhead). G, Glio-interstitial cell. (e) *Hyridella depressa* palp (HBF, TEM). A muscle fibre in an artery wall is pictured, showing a connection between a glio-interstitial cell (G) and a lateral projection from the muscle (M).

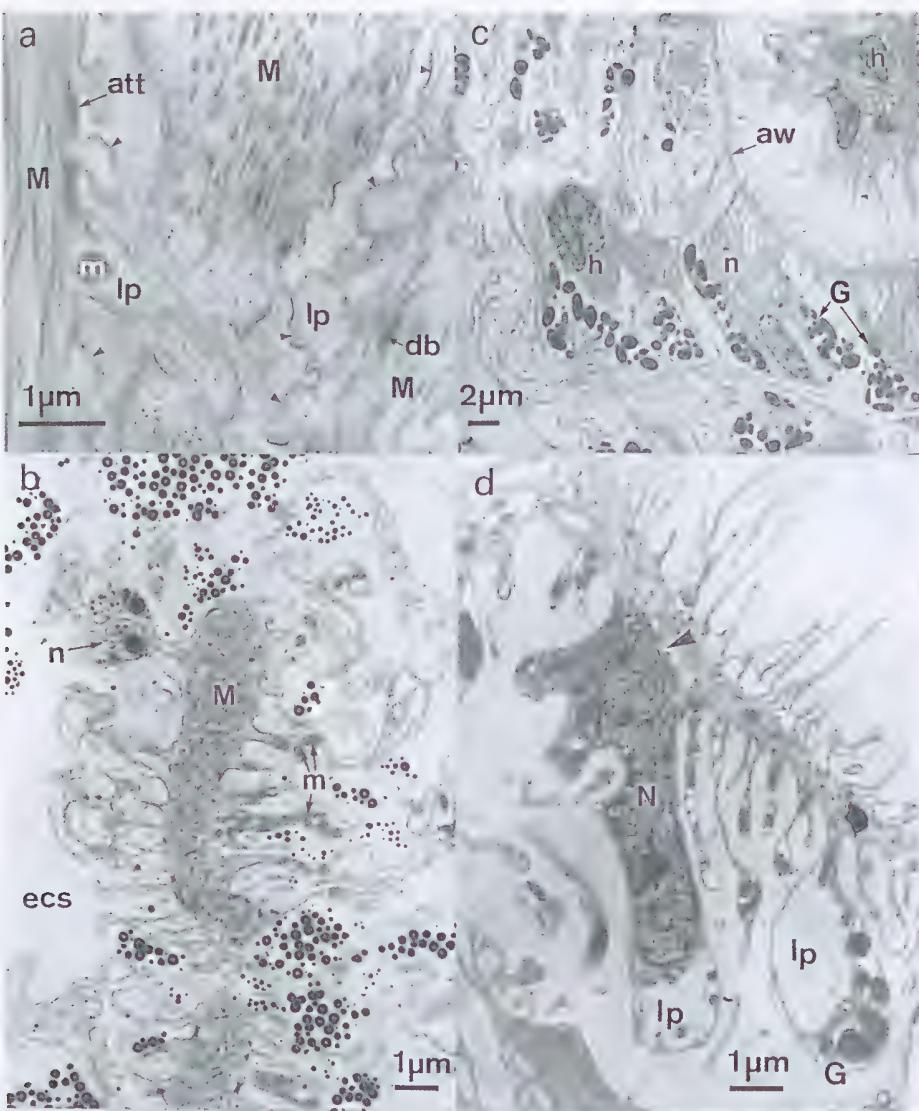


Fig. 5. Muscle. (a) *Hyridella depressa* mantle margin (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). The dense muscle bands at the margin of the mantle contain large muscle fibres (M) with short lateral cytoplasmic projections (lp) and few mitochondria (m). Subsarcolemmal cisternae (arrowheads) lie parallel to the plasma membrane in the lateral projections. Thick and thin filaments are irregularly arranged and dense attachment plates (att) connect the filaments to the plasma membrane. The extracellular spaces contain many collagen fibres. (b) *Velesunio ambiguus* mantle central zone (HBF, TEM). The muscle fibres traversing the mantle (M) have large lateral cytoplasmic projections containing many mitochondria (m) and often form connections with nerves (n) and glio-interstitial cells. Collagen fibres and many small granules are present in the extracellular space (ecs). (c) *Velesunio ambiguus* palp (HBF, TEM). Montage of artery wall (aw). The numerous lateral processes on the muscle cells make connections with nerves (n) and glio-interstitial cells (G). h, Haemocytes. (d) *Velesunio ambiguus* palp (HBF, TEM). A nucleus (N) in an artery wall shows deep convolutions in the nuclear membrane (arrowhead), presumably to allow stretching and contraction. The large lateral cytoplasmic processes (lp) probably contained glycogen. G, Glio-interstitial cell.

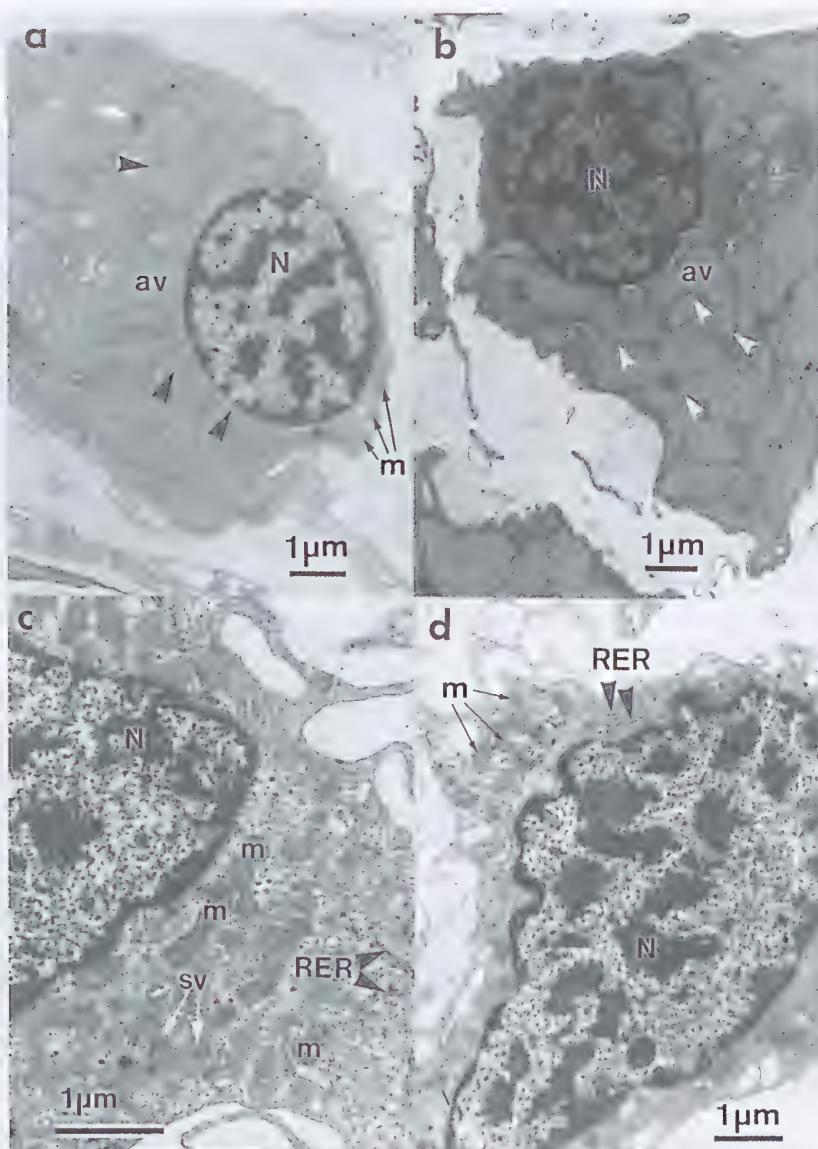


Fig. 6. Haemocytes. (a) *Hyridella depressa* mantle central zone (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). Haemocyte with large amorphous vesicles (av). The cytoplasm contains a prominent electron-lucent tubule system (black arrowheads). The white arrow indicates an electron-dense granule within an amorphous vesicle; these were very rarely observed. N, Nucleus; m, mitochondria. (b) *Hyridella depressa* palp (cacodylate-buffered fixation, TEM). When fixed with cacodylate buffer, the haemocytes with large amorphous vesicles (av) had denser cytoplasm and the electron-lucent tubules (white arrowheads) were not as prominent. (c) *Valesunio ambiguus* palp (HBF, TEM). A haemocyte with a number of small medium-density vesicles (sv) in the cytoplasm. Some rough endoplasmic reticulum is present (RER), but there are few electron-lucent vesicles. N, Nucleus; m, mitochondria. (d) *Valesunio ambiguus* palp (HBF, TEM). A haemocyte with some rough endoplasmic reticulum (RER), mitochondria (m) and electron-lucent vesicles and very few small medium-density vesicles. N, Nucleus.

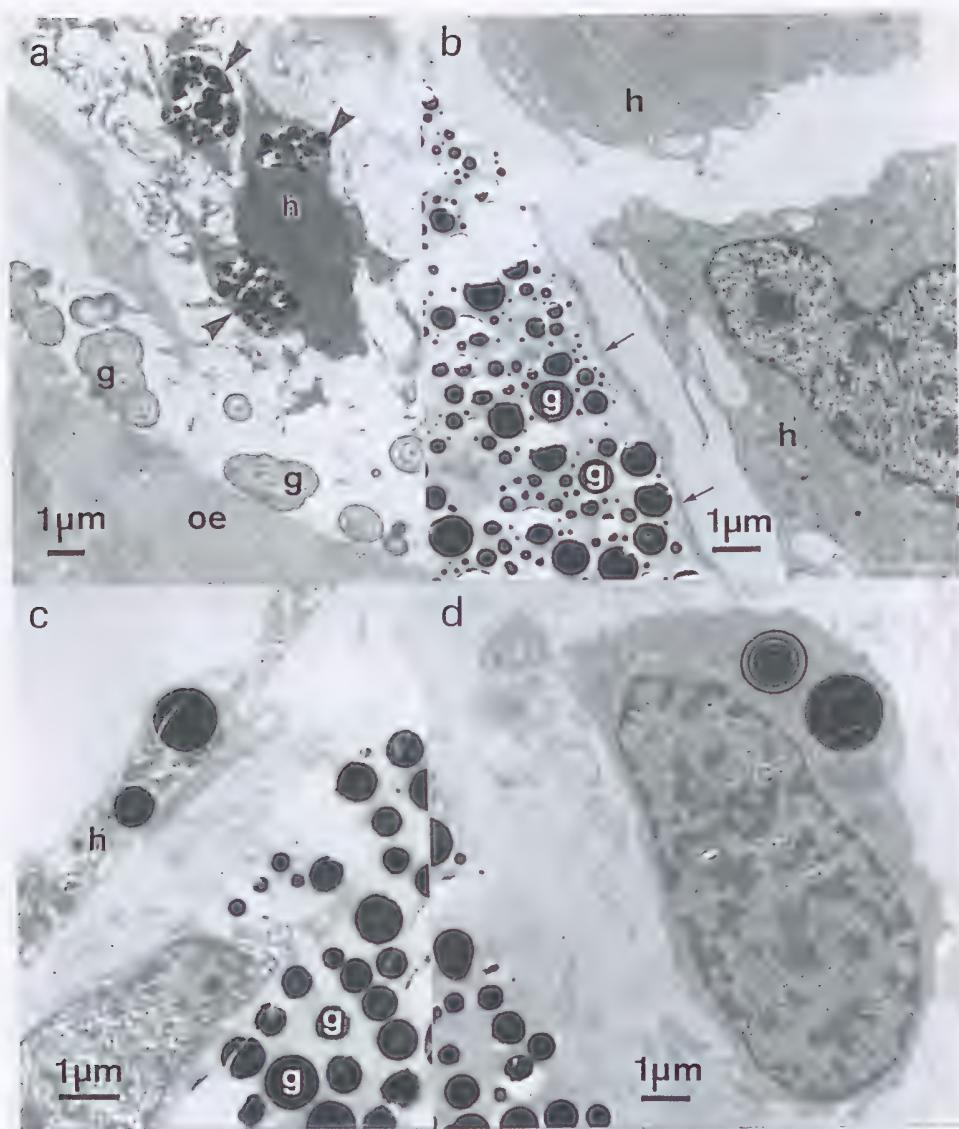


Fig. 7. Granules. (a) *Hyridella depressa* mantle central zone (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). Laminar granules (g) lie under the outer epithelium (oe). Some electron-dense granules within lysosomes (arrowheads) in a haemocyte (h) appear similar to the extracellular granules in (b-d). (b) *Velesunio ambiguus* palp (HBF, TEM). A cluster of electron-dense granules (g) is partially enclosed by long cytoplasmic extensions (arrows). The figure also shows two haemocytes (h), one with large amorphous vesicles and one with small vesicles. (c) *Hyridella depressa* palp (HBF, TEM). A cluster of extracellular granules (g). Similar granules are visible inside a neighbouring haemocyte (h). (d) *Hyridella depressa* palp (HBF, TEM). A haemocyte with intracellular laminar granules.

reticulum were usually present, often lying parallel to the nuclear membrane. These cells sometimes contained residual bodies and sometimes intracellular electron-dense granules, either free in the cytoplasm or within residual bodies (Fig. 7a,c,d). Haemocytes with

residual bodies and intracellular granules were more common in *H. depressa* than in *V. ambiguus*.

Calcified granules

As noted above, the mantle and palps contained varying quantities of orange-pigmented electron-dense granules. Most granules were extracellular, 0.1–1 µm in diameter and with one or two laminae and occurred in large clumps, usually among vesicular cells (Figs 1b, 2b,c). Granules were also scattered in the interstitial tissue (Fig. 7). Only the smaller groups of granules could be photographed using TEM; larger clumps generally disintegrated during sectioning or in the electron beam.

There were some differences between the species in the appearance of the granules. In *H. depressa* mantle, in which the granules were generally very numerous, the majority of granules occurred as large clusters of small granules, but there were also many multilamellar granules (Figs 1d, 7a). In *V. ambiguus* mantle, in which few granules were visible macroscopically, the granules were generally small and scattered among the lateral processes of muscle cells (Fig. 5b).

The smaller granules did not stain with toluidine blue in LM sections, but appeared pale yellow and refractile. Some of the larger granules sectioned in the mantle central zone of *H. depressa* stained pale pink or blue with toluidine blue. Using SEM, the granules in the large clumps appeared as spheres, 0.5–3 µm in diameter. Often filopodia could be seen wrapped around the clumps (Fig. 7b).

Intracellular electron-dense granules of various sizes and shapes were often observed in both species, either free in the cytoplasm (Fig. 7c,d) or in structures resembling tertiary lysosomes (Fig. 7a). In EM, some of these granules closely resembled the extracellular granules in shape and laminar structure (Fig. 7a,c). However, in the toluidine blue-stained LM sections, many of the smaller intracellular granules stained dark blue, so their composition was probably different from the extracellular granules. Large laminar intracellular granules were occasionally observed in TEM sections of *H. depressa* mantle (Fig. 7d), but they could not be positively identified in the LM sections.

Epithelia

Inner epithelium of mantle

The inner epithelium facing the mantle cavity had three main types of cells: epidermal cells (cells with microvilli and no cilia); ciliated cells (with cilia and microvilli); and glandular cells (terminology after Simkiss (1988)). Cell heights were very variable, ranging from 10 to 30 µm, and the cells rested on a basement membrane ranging in thickness from 3 to 8 µm.

The epidermal cells (Fig. 8a,b,d) generally had pale-staining nuclei, often lobed, with scattered patches of darker chromatin and a large nucleolus. The microvilli ranged from 0.4 to 1.0 µm in length. In the apical cytoplasm, there were often many vesicles containing material of variable electron density. These vesicles were usually elongated (Fig. 8a,b), but they were much more rounded in the central zone of the mantle in *V. ambiguus* (Fig. 8d). The vesicles sometimes appeared to make contact with the plasma membrane, but it was not possible to determine whether they were taking up or releasing material. In both species, there were also numerous small clear vesicles, mitochondria, short lengths of rough endoplasmic reticulum and multivesicular bodies (Fig. 8a,b,d).

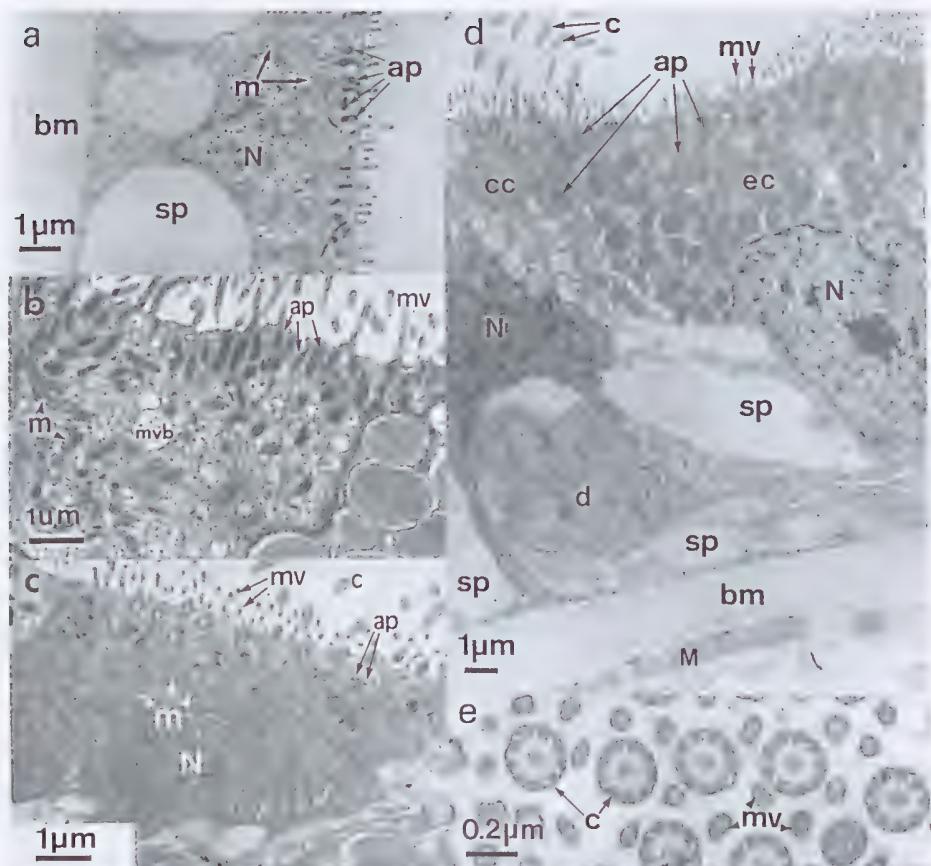


Fig. 8. Inner epithelium of the mantle. (a) *Hyridella depressa* mantle epidermal cell (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). The epidermal cells have apical microvilli, and rest on a thick basement membrane (bm). Large basal spaces (sp) can be seen to connect with the extracellular space in some sections. Small dense-cored vesicles (ap) are present in the apical cytoplasm. N, Nucleus; m, mitochondria. (b) *Hyridella depressa* mantle epidermal cell (HBF, TEM). Detail of apical cytoplasm, showing microvilli (mv), dense elongated apical vesicles (ap), mitochondria (m), a multivesicular body (mvb) and numerous small clear vesicles. (c) *Hyridella depressa* mantle ciliated cell (HBF, TEM). The mitochondria (m) in ciliated cells are more numerous than in epidermal cells. The cytoplasm and nucleus of ciliated cells tend to stain more densely than in epidermal cells (cf. neighbouring epidermal cell in the top left corner of the figure). c, Cilium; mv, microvilli; ap, apical vesicles; N, nucleus. (d) *Velesunio ambiguus* inner epithelium of the mantle (HBF, TEM). On the right is an epidermal cell (ec) showing microvilli (mv), a pale-staining nucleus and cytoplasm and rounded apical vesicles (ap). On the left is a ciliated cell (cc) with cilia (c), microvilli, more densely staining cytoplasm and nucleus (N) and a mixture of rounded and elongated apical vesicles. The basal spaces (sp) contain cell debris (d) and myelin figures. The thick basement membrane (bm) overlies nerves and muscles (M). (e) *Hyridella depressa* (HBF, TEM). Detail of cilia (c), showing a pair of central tubules and a ring of nine groups of tubules. mv, microvilli.

The cytoplasm and nucleus of the ciliated cells generally stained more densely than in the epidermal cells, in both ultrathin and semithin sections (Fig. 8c,d). In addition, the microvilli were slightly longer (0.6–1.4 µm) and mitochondria were more common in ciliated cells. In both species, the apical vesicles were generally elongated (Fig. 8c,d). The cilia showed the usual 9+2 microtubular structure (Fig. 8e).

The glandular cells of the inner epithelium contained many vesicles filled with finely textured secretory material (Fig. 9a). In semithin sections stained with Methylene blue–Azure II–Basic Fuchsin, this material varied from large, dark pink-staining globules to paler pink, flocculent material. In some cells, both types of material were present. In the basal region of the glandular cells, there were often large dilated cisternae of rough endoplasmic reticulum filled with fine granular material (Fig. 9b).

In the basal portion of the inner epithelium of the mantle, there were many large extracellular spaces that appeared to communicate with the extracellular fluids below the basement membrane (Figs 8a,d, 9a). These often contained degenerating cellular components or blood cells with large amorphous vesicles in the cytoplasm.

Outer epithelium of mantle

In both *V. ambiguus* and *H. depressa*, most cells in this epithelium were cuboidal epidermal cells 10–15 µm high and 8–10 µm wide, lying on a basement membrane (Fig. 9c). The apical surface of the cells was covered by microvilli, 0.5–1.0 µm long. Nuclei were large and usually central or apical, with prominent nucleoli. Much of the cell was filled with fine granular glycogen-like storage material, with thin layers of darker cytoplasm around the periphery, surrounding the nucleus and in strands through the granular material. There were scattered mitochondria in the cytoplasmic strands and occasional lipid-like droplets.

Glandular cells were occasionally observed in the outer epithelium (Fig. 9d), but they were relatively rare. There were no ciliated cells.

Epithelia of the mantle folds

The outer mantle fold and the outer surface of the middle fold had no ciliated or glandular cells. The epidermal cells of the outer mantle fold were short with deeply infolded basal membranes. The lateral membranes between adjoining cells were often deeply convoluted. The epidermal cells of the periostracal groove contained large numbers of vesicles, often containing material with a dense core, which appear to have a secretory function (not shown).

Cells in the middle and inner mantle folds were predominantly epidermal cells and glandular cells, with scattered ciliated cells. Glandular cells in this region often extended through the basement membrane into the subepidermal region. Spherical or irregular dark-staining pigment granules were present in the mantle margin epithelium, particularly in the region of the mantle near the inhalant and exhalant openings, where the mantle shows dark pigmentation (Fig. 10a).

Palps

The outer epithelium of the palps (Fig. 10b) was similar to the inner epithelium of the mantle, with which it is continuous. In areas where the cells formed protuberances (Fig. 2d), the apical bulges of cytoplasmic material contained fine granular material, probably glycogen, and few organelles (Fig. 10c). The ratio of ciliated cells to epidermal cells varied in different areas, from a complete cover of cilia to scattered tufts.

The ridged surfaces of the palps were covered with ciliated cells up to 50 µm tall, interspersed with glandular cells.

Discussion

The mantle and palps in these hyriid mussels resemble those of the unionids in general structure and in the presence of large quantities of extracellular calcified granules in the

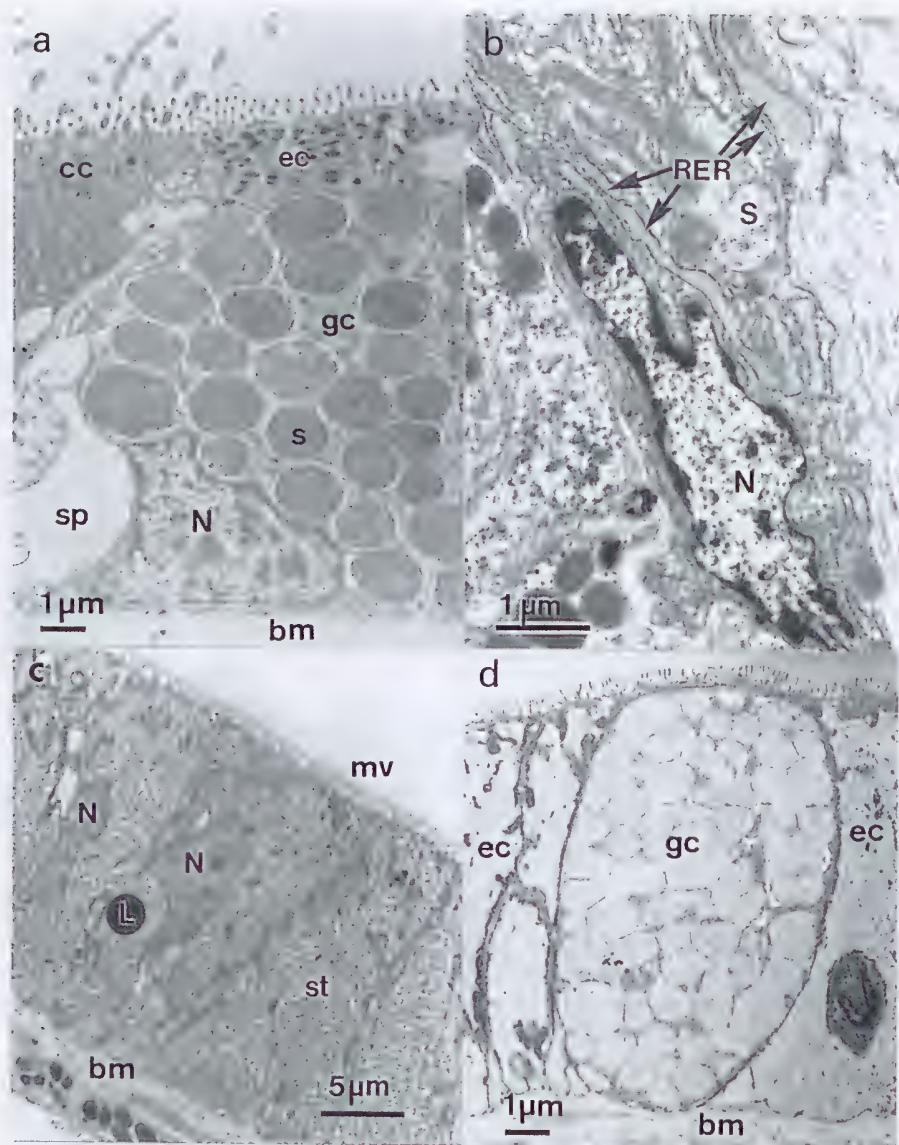


Fig. 9. Mantle epithelia. (a) *Hyridella depressa* mantle central zone, inner epithelium (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). Glandular cell (gc) showing vesicles of finely textured secretory material (s), basal nucleus (N). cc, ec, Neighbouring ciliated and epidermal cells, respectively; bm, basement membrane; sp, basal space. (b) *Velesunio ambiguus* mantle margin (HBF, TEM). Detail of the basal region of a subepidermal glandular cell showing dilated rough endoplasmic reticulum (RER) cisternae (arrows) and a vesicle of secretory material (S). N, Nucleus. (c) *Velesunio ambiguus* mantle (HBF, TEM). Montage of the outer mantle epithelium. The epidermal cells are almost completely filled with fine granular storage material (st; probably glycogen), with thin strands of cytoplasm around the periphery and an occasional lipid-like droplet (L). Microvilli (mv) cover the apical surface, which lies against the shell. bm, Basement membrane; N, nucleus. (d) *Velesunio ambiguus* mantle central zone, outer epithelium (HBF, TEM). A glandular cell (gc) filled with secretory material, ec, Epidermal cells; bm, basement membrane.

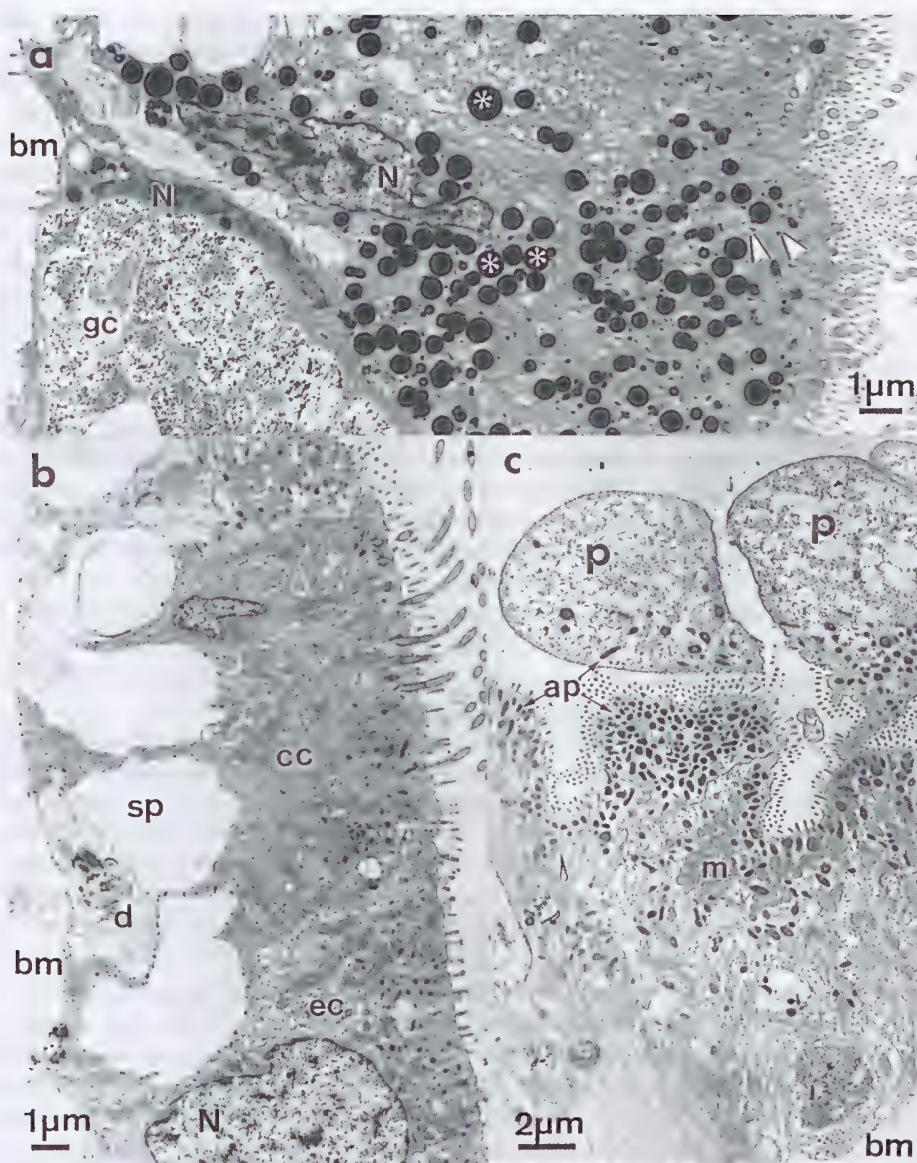


Fig. 10. Mantle and palp epithelia. (a) *Hyridella depressa* mantle (HEPES-buffered fixation (HBF), transmission electron microscopy (TEM)). Pigmented epithelium near inhalant opening. Numerous round, electron-dense pigment granules with no limiting membrane (*) lie in the cytoplasm. White arrowheads, apical vesicles; bm, basement membrane; gc, glandular cell; N, nucleus. (b) *Hyridella depressa* outer epithelium of palp (HBF, TEM). The epidermal and ciliated cells (ec and cc, respectively) are similar in general appearance to the inner mantle epithelium (see Fig. 8). bm, Basement membrane; d, cell debris; N, nucleus, sp, basal space. (c) *Velesunio ambiguus* outer epithelium of palp in a region comparable with that shown in Fig. 2d (HBF, TEM). Apical protuberances (p) contain mainly granular glycogen-like material and are largely free of organelles. ap, Apical vesicles; bm, basement membrane; m, mitochondria.

connective tissue (Beedham 1958; Istin and Masoni 1973; Petit *et al.* 1978; Pynnönen *et al.* 1987; Machado *et al.* 1988; A. E. Colville and E. B. Andrews, unpublished data). However, the majority of granules occurred in clusters or among lateral processes of muscle cells rather than enmeshed in collagen fibres as in the unionid *Anodonta*.

The vesicular cells in *H. depressa* and *V. ambiguus* appear similar to the vesicular, or Leydig, cells described in many molluscs (Sminia 1972; Gabbott 1983; Pipe 1987; Beninger *et al.* 1995; Eckelbarger and Davis 1996; Berthelin *et al.* 2000). These cells store large amounts of glycogen and act as a nutrient reserve (Lowe *et al.* 1982; Pipe 1987).

The structure of the nerves and glio-interstitial cells was similar to that described for *Anodonta* (Gupta *et al.* 1969; Nakao 1975), although the glial fibres described by Gupta *et al.* (1969) were not apparent in the cells examined here. The muscles in the mantle and palps were the classic smooth muscle described by Chantler (1983), with no apparent cross or oblique striations. They are similar to the type B cells of the smooth muscle classification system of Matsuno (Paniagua *et al.* 1996) with regard to the thick filament size and positioning of cell organelles, but the nuclei are peripherally placed rather than central.

There have been numerous attempts to classify bivalve haemocytes (Cheng 1981; Auffret 1988; Hine 1999). Hine (1999) concluded that there is evidence for a number of forms of granular and agranular haemocytes and that the types and numbers of haemocytes present may differ between bivalve families and even between individual animals.

In these hyriid mussels, the granulocytes with large amorphous vesicles formed a well-defined population and were the most common haemocytes observed. Similar cells are present in *Anodonta grandis* (Silverman *et al.* 1989) and *Anodonta cygnea* (Machado *et al.* 1988).

The remaining haemocytes were rather variable in form. The presence of tertiary lysosomes suggests that these cells are more phagocytic than the haemocytes with large amorphous vesicles, but it is possible that phagocytic ability varies with the nature of the material to be phagocytosed (Hine 1999). Further study is needed to characterise the different forms.

Mineralised granules are commonly observed in invertebrate tissues, but most are intracellular or are expelled as a form of excretion, so extracellular calcium- and phosphorus-rich granules in freshwater mussels are unusual (Brown 1982). When prepared by standard aqueous techniques, most of the granules in *H. depressa* and *V. ambiguus* resemble those found in other freshwater mussel species in appearance and chemical composition, with large amounts of Ca and P and lesser amounts of Fe and Mn and other trace constituents detected (Roinel *et al.* 1973; Davis *et al.* 1982; Silverman *et al.* 1983; Jeffree and Simpson 1984; Steffens *et al.* 1985; Pynnönen *et al.* 1987; Colville 1994). Some studies of unionids have reported the presence of carbonate in some granules (Moura *et al.* 1999), but Jeffree *et al.* (1993) considered that the granules in *H. depressa* and *V. ambiguus* were probably mainly phosphate.

However, recent studies indicate that, in cryoprepared tissues, the annular structure of the granules is not visible and the proportion of Fe is markedly increased, so aqueous preparation probably results in artefacts caused by loss and redistribution of elements (Vesk and Byrne 1999; Byrne 2000). Some intracellular granules that could be cut relatively easily in thin sections and that stained blue with toluidine blue in the thick sections are probably not calcium phosphate, but may have a sulfur-based composition (Adams *et al.* 1997; Vesk and Byrne 1999).

Phosphate-rich granules tend to be associated with so-called 'hard acid' or 'class A' metals, such as calcium, magnesium and barium, whereas granules rich in sulfur (such as

are common in oyster haemocytes) exhibit a different chemistry and tend to be associated with 'soft acid' or 'class B' metals, such as copper and mercury (Nieboer and Richardson 1980; Brown 1982; Taylor and Simkiss 1989).

The origin of the granules in these mussels has been the subject of several studies. Silverman *et al.* (1989) considered that the granules in *Anodonta grandis* are formed within the amorphous vesicles of haemocytes, which they termed 'concretion-forming cells' or CFCs. The granulocytes in the hyriid mussels in the present study look very similar to the CFCs but, although they also occasionally contained small electron-dense bodies, there was no evidence of a sequence of granule formation comparable with that reported in *Anodonta* (Silverman *et al.* 1989). In *H. depressa* and *V. ambiguus*, most of the intracellular electron-dense granules were in haemocytes without large amorphous vesicles (present study and from inspection of the figures in Byrne (2000)), so these cells are a more likely source. It was also notable that the large granule clumps were usually associated with vesicular cells and were surrounded by filopodia that resembled the thin outer layer of cytoplasm around the vesicular cells. This raises the possibility that vesicular cells may also be involved in some way with granule production.

The ultrastructure of the epithelia of the mantle and palps is very similar in the two species of mussel, with minor differences in the appearance of the apical vesicles of the epidermal and ciliated cells in the inner mantle and palps.

The outer mantle epithelium (nearest the shell) is responsible for secretion of the inner layers of the shell (Istin and Masoni 1973). The outer epithelial cells are similar in structure to the outer epidermal cells in *Anodonta* (Machado *et al.* 1988; A. E. Colville, personal observation), *Cardium edule* (Cardiidae), *Nucula sulcata* (Nuculidae), *Mytilus edulis* (Mytilidae) (Bubel 1973) and the freshwater Asiatic clam *Corbicula fluminea* (Corbiculidae) (Lemaire-Gony and Boudou 1997). In these species, the outer epithelial cells appear to function mainly to store glycogen. There was little cellular machinery to suggest active secretion of shell material. In contrast, outer mantle epidermal cells from *Pinctada radiata* (Pteriidae) and *Isognomon alatus* (Isognomonidae), which are both in the superfamily Pteriacea, contain numerous mitochondria and endoplasmic reticulum cisternae (Nakahara and Bevelander 1967). This difference in cellular structure may reflect phylogenetic differences, seasonal variation or functional differences.

Beedham (1958) found that mucous cells occurred in large numbers in the outer epithelium of *A. cygnea*. Machado *et al.* (1988) concluded that the secretory cells in *Anodonta* were probably responsible for secretion of material for the organic matrix of the shell. In contrast, glandular cells in the outer epithelium of the mantle were rare in *H. depressa* and *V. ambiguus*.

Growth rates in *H. depressa* and *V. ambiguus* of comparable sizes to the animals examined in the present study are very low (Colville 1994), so it is possible that the inactive appearance of the outer epidermal cells and the small number of glandular cells reflect a low rate of shell deposition in these specimens.

One cell type that was not observed in the present study was the rhogocyte or pore cell, which is diagnostic of molluscs (Haszprunar 1996) and which can accumulate large amounts of glycogen and appear similar to vesicular cells (Skelding and Newell 1975; Beltz and Gelperin 1979; Jones and Bowen 1979). However, slit complexes were not evident in any cells examined in *H. depressa* and *V. ambiguus*. Rhogocytes may undergo cyclical changes in the percentage of membrane showing grooves (Baleydier *et al.* 1969), so it is possible that there were no cells in the appropriate phase when these mussels were collected. It is also possible that rhogocytes are present in the mantle or palps in heavily calcified areas

where the specimens disintegrated in the electron beam before they could be examined; further studies of decalcified tissue would be required to investigate these regions.

The freshwater mussels *V. ambiguus* and *H. depressa* were, by and large, very similar in terms of general histology and ultrastructure of the mantle and palps. The major difference was the greater abundance of granules in the central zone of the mantle of *H. depressa*, which was sometimes associated with an increased density of connective tissue cells and fibres. There were slight differences in the apical vesicles in the cells of the inner mantle and palp epithelia.

Byrne (2000) speculated that the distribution of granules in the interstitial tissues of mussels may be a useful character in phylogenetic analyses. She contrasted the granule distribution in *H. depressa* (Hyriidae) and *Margaritifera margaritifera* (Margaritiferidae), which have extensive aggregations in the mantle and few in the gills, with unionids such as *Anodonta* and *Ligumia*, where the granules occur predominantly in the gills. Unfortunately, this division is not so clear-cut because, within the subfamilies of the Hyriidae, there is variation in the abundance of granules in mantle and gills (Ch'ng-Tan 1968; Colville 1994). However, it would be of considerable interest to determine whether granules are present in the Etherioidea, because this may provide more information about the phylogenetic relationships among the superfamilies.

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Phylogenetic assessment of characters proposed for the generic classification of Recent Scissurellidae (Gastropoda: Vetigastropoda) with a description of one new genus and six new species from Easter Island and Australia

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Abstract

Twenty-five nominal generic names have been proposed for the approximately 150 Recent species described in the family Scissurellidae (Mollusca: Gastropoda: Vetigastropoda). The generic diagnosing characters have not been uniformly applied and the value of these characters for scissurellid classification remains to be demonstrated. Here, the characters used are reviewed, including those of the shell, slit and selenizone, radula, soft tissue anatomy and histology. An overview of the state of our knowledge of these various character sets is given. Exploratory phylogenetic analysis reveals that scissurelline protoconch sculpture is highly homoplastic. The character conflict between protoconch sculpture and slit/foramen in *Scissurella* and *Sinezona* is resolved in favour of the latter characteristic. The closure of the slit to a foramen is governed by a driven trend. Other characteristics cited as diagnostic for certain genera are highly homoplastic, including the umbilical funiculus of *Praescissurella* Lozouet, 1998 and the smooth protoconch of *Sukashitrochus* Habe and Kosuge, 1964. *Sukashitrochus*, diagnosed by strong spiral sculpture on the base of the shell, is transferred from Anatominae to Scissurellinae and '*Scissurella*' *dorbignyi* Audouin, 1826 is assigned tentatively to this genus. *Coronadoa simonsae* Bartsch, 1946 shows a typical scissurelline radula with five laterals, contrary to earlier reports. Several recently proposed genera are synonymised here: *Anatoma* (+ *Hainella* Bandel, 1998), *Scissurella* d'Orbigny, 1824 (+ *Maxwellella* Bandel, 1998; *Reussella* Bandel, 1998, *Praescissurella*), *Sinezona* (+ *Daizona* Bandel, 1998), *Thieleella* Bandel, 1998 (+ *Pagodella* Bandel, 1998: *nomen nudum*). The newly described *Satondella* Bandel, 1998, and *Thieleella*, are considered valid. *Ariella* Bandel, 1998, is conservatively retained. *Scissurona* is synonymised under *Incisura*. Cladistic analysis based on shell and radular characteristics, using autapomorphies to code inapplicables, revealed several patterns. The two main lineages in Scissurellidae *sensu lato* are Scissurellinae (*Coronadoa*, *Incisura*, *Satondella*, *Scissurella*, *Sinezona*, *Sukashitrochus*) plus Anatominae (*Anatoma*, *Thieleella*) and Sutilzoninae (*Sutilzona*) plus Temnocinclinae (*Temnocincis*, *Temnozaga*) plus Larocheinae (*Larochea*, *Larocheopsis*, *Trogleconcha*). These two lineages are characterised by differences among lateral teeth on the radula. *Depressizona* n. gen. is placed in its own subfamily, Depressizoninae n. subfam. One new genus and five new species of scissurellids are described from Easter Island (*Depressizona exorum* n. gen. and n. sp., *Anatoma raineri* n. sp., *Scissurella alto* n. sp., *Sinezona zimmeri* n. sp., *Satondella senni* n. sp.) and one new species from Australia (*Trogleconcha christinae* n. sp.). The calyptraeiform *Depressizona* n. gen. exhibits a new type of shell morphology for the family. The scissurellids from Easter Island show a stronger biogeographic affinity with Polynesia and the Central Pacific than with the eastern Pacific.

Additional keywords: autapomorphy, cladistics methodology, evolutionary patterns, generic concepts, inapplicables.

Introduction

The vetigastropod Scissurellidae is of worldwide distribution and has a fossil record reaching back to the mid-Triassic (Bandel 1998). The family is found from the shallow intertidal to the deep sea, including representatives at hydrothermal vents. The family is composed of

approximately 150 described species. The number of undescribed species is appreciable; Marshall (2002) considered only half the scissurellid fauna of New Zealand described and a number of Australian species have not yet been formally recognised (Jansen 1999; D. L. Geiger and P. Jansen, unpublished data). The Recent species are classified in 25 nominal genera: *Anatoma* Woodward, 1859; *Schizotrochus* Monterosato, 1877; *Ariella* Bandel, 1998; *Coronadoa* Bartsch, 1946; *Depressizona* n. gen.; *Diazona* Bandel, 1998; *Hainella* Bandel, 1998; *Incisura* Hedley, 1904; *Larochea* Finlay, 1927; *Larocheopsis* Marshall, 1993; *Maxwellella* Bandel, 1998; *Pagodella* Bandel, 1998; *Reussella* Bandel, 1998; *Satondella* Bandel, 1998; *Schismope* Jeffreys, 1856; *Scissurella* d'Orbigny, 1824; *Scissurona* Iredale, 1924; *Sinezona* Finlay, 1926; *Sukashitrochus* Habe and Kosuge, 1964; *Sutilizona* McLean, 1989; *Temnocinclus* McLean, 1989; *Temnozaga* McLean, 1989; *Thieleella* Bandel, 1998; *Troglonconcha* Kase and Kano, 2002; *Woodwardia* Crosse & Fischer, 1861. The fossil genus *Zardinitrochus* Bandel, 1998, with sole species *Z. suessi* (Klipstein in Kittl, 1891) from the early Triassic is too poorly preserved to allow inclusion in the present study. Recently, a number of additional species and genera have been introduced (Bandel 1998). Kase and Kano (2002) and Marshall (2002) critically reviewed some of these taxa, although there has been no encompassing review of the genera.

The generic concepts and the application of generic names is rather difficult, particularly because different characteristics and characteristic combinations have been used to describe and diagnose the genera. Furthermore, the assignment of many species to any of the described genera is uncertain. For one, the characteristics necessary for such an assignment are insufficiently documented or entirely unknown, which is particularly the case for Anatominae. The quality of available specimens often makes generic assignments impossible. In addition, intraspecific variation of characteristics has rarely been documented, further complicating the evaluation of usefulness of characteristics and character states applied to the generic classification of scissurellid species. It is the purpose of the present review to discuss the available characteristics, their intra- and interspecific variability and to provide an overview of the present state of knowledge with respect to these characteristics for the species in the literature (Appendix 1). This overview will highlight the areas of greatest need for documentation and further research. Based on this information, the generic concepts are evaluated using data from shell morphology and radula in a phylogenetic approach.

Information on the anatomy of Scissurellidae is rather limited. The external anatomy has been described for some taxa (e.g. *Sukashitrochus* sp.: Haszprunar 1988, *Anatoma* s.l. sp.: Sasaki 1998, *Troglonconcha ohashii*: Kase and Kano 2002). The internal anatomy is known only from a handful of species, with a bias towards the more aberrant types within Scissurellidae (*Incisura*: Pelseneer 1899; Bourne 1910; *Scissurella*: Pelseneer 1899; *Temnocinclus*, *Temnozaga*, *Sutilizona*: Haszprunar 1989; *Anatoma* s.l. sp.: Sasaki 1998). There is a great need to engage in basic anatomical and histological studies (Herbert 1986; Hickman 1999; Kase and Kano 2002) and this is an ongoing project of the present author. Some of the known variation is summarised below.

Both papillate (Scissurellinae, Anatominae) and non-papillate cephalic and epipodial tentacles (Larocheinae, Temnocinclinae, Sutilizoninae) are found (Sasaki 1998), whereas *Troglonconcha* has non-papillate epipodial tentacles, but papillate cephalic tentacles (Kase and Kano 2002). The particular type of papillae has not been specified and it is not known whether more than one type of papillae is found in Scissurellidae. Bipectinate gills are found in Scissurellinae and Anatominae, whereas a monopectinate condition is encountered in Larocheinae, Sutilizoninae and Temnocinclinae. Although

most Scissurellidae are of such a small size that diffusion should be able to fulfill respiratory function, all species investigated have gills and a well-developed heart (Pelseneer 1899; Bourne 1910; Haszprunar 1989; D. L. Geiger, unpublished data: *Sinezona rimuloides* Carpenter, 1865). The shell may act as a barrier for diffusion. Bursicles on the gills have been confirmed in *Anatoma* s.l. sp. (Sasaki 1998), in *Temoncinclis*, *Temnozaga* and *Sutilizona* by Haszprunar (1989) and in *Incisura* as 'ciliated canal of dorsal ridge' (Bourne 1910: figs 16–18). Eyes are absent in Sutilizoninae and Temnocinclinae. Sperm ultrastructure has been documented for *Sinezona* sp., which showed a highly derived condition within Vetigastropoda (Healy 1990). The value of scissurellid sperm for generic classification has yet to be explored.

In Appendix 1, the specific epithets used are those of the authors cited, which may not agree with the original descriptions. Misidentification of specimens is commonplace in Scissurellidae (e.g. Kase and Kano 2002; Marshall 2002). Known synonyms and misidentifications, as well as obvious mistakes, have been taken into account; however, it is beyond the scope of this contribution to engage in a global revision of the family. Selected fossil species have been included if they help in clarifying the classification of the Recent species or are otherwise significant. The generic placement of the species, including one new genus and five new species from Easter Island and one new species of *Troglonconcha* from Australia, is performed according to the conclusion of the phylogenetic analysis presented here.

Materials and methods

The literature of Scissurellidae was surveyed with a bias towards the more modern and readily accessible titles, particularly those with scanning electron micrographs (SEM). The specimens at the Australian Museum, Sydney, were investigated for intraspecific variability using the in-house SEM facility (LEO 435VP; Carl Zeiss, Oberkochen, Germany), as well as the Cambridge Stereoscan 360 (Carl Zeiss) at the University of Southern California, Los Angeles. Dry specimens were cleaned in a mild detergent solution using a sonicator. Protoconch size given in the species description is the maximum size including varices and other sculptural elements. Radulae were extracted from dry specimens with an approximate 10% NaOH or KOH solution at 35–45°C overnight. Shells of the very specimen from which the radulae were extracted were imaged by SEM. A more detailed discussion of handling small radulae is in preparation.

Exploratory phylogenetic analysis was performed with PAUP* (Swofford 2001), constraining the monophyly of outgroup and ingroup. All 18 binary and multistate characters were unordered and polarised by outgroup comparison. Inapplicables were coded as autapomorphies, which forces the algorithm not to infer any relationships with other terminal taxa, unlike the missing data treatment advocated by Strong and Lipscomb (2000). When inapplicables are coded as missing data, the phylogenetic algorithm will assume one of the existing character states during character-state optimisation and introduce unobserved synapomorphies (Geiger 2002a). The only effect of coding inapplicables as autapomorphies is that tree length and the consistency index are increased. Because these two metrics by themselves do not affect the topology recovered, these effects are considered inconsequential, unlike those produced by unobserved synapomorphies. The data matrix is given in Appendix 2. For the 34-taxon analysis, 10000 random addition sequence replications were run and a majority-rule consensus tree was calculated from all trees.

For the 87-taxon analysis, all equally parsimonious resolutions could not be stored in memory (110 MB allocated, maxtrees = 100000), because the number of informative character states was far lower than the number of taxa (37 for 87 taxa, with inapplicables-as-autapomorphies excluded). Following the topology from the 34-taxon analysis, the monophyly of Scissurellinae was constrained. Thirty different random addition sequence replications were run and a 50% majority-rule consensus tree was calculated from all equally most parsimonious resolutions.

Statistical analysis was performed with StatisticaMac 4 (Statsoft 1991). Multiletter abbreviations for generic names are used for genera with identical initial letter in accordance with recommendation 25A of the International Code of Zoological Nomenclature (ICZN).

Institutional abbreviations and text conventions

AMNH	American Museum of Natural History, New York, NY, USA
AMS	Australian Museum, Sydney, NSW, Australia
ANSP	Academy of Natural Sciences, PA, USA
BMNH	The Natural History Museum, London, UK
LACM	Natural History Museum of Los Angeles County, CA, USA
UMUT	The University Museum, The University of Tokyo, Japan
†	fossil species
<i>taxon</i>	taxon as used by cited author(s)
taxon	informal name
CI	consistency index
RI	retention index
OD	Original designation
SD	Subsequent designation
M	Monotypy

Systematics

In the systematic section, I will make use of some conclusions only obtained through the phylogenetic analysis presented in the second part of this contribution. It applies particularly for generic placement of a number of species mentioned. It should be kept in mind that the systematics and the phylogenetics section inform one another reciprocally.

I use here the genus *Anatoma* s.l. for species that cannot be assigned to the two genera in Anatominae, *Anatoma* and *Thieleella*, because the information on protoconch sculpture necessary for placement is not available.

Nomenclature

The authority of *Ariella haliotimorpha*, *Scissurella eocaenica* and *Sci. peyrerensis* was indicated by Bandel (1998) as '(Lozouet, 1986), n. sp.'. Marshall (2002), as the first reviser, has used 'Bandel, 1998' as the author and his opinion is followed here. Lozouet intended to describe the taxa himself, but even his description of *Sinezona haliotimorpha* Lozouet 1998, was preceded by Bandel's by three months (Lozouet 1998).

One specific epithet introduced by Bandel (1998) does not conform with the ICZN rules. '*Maxwellella gründeli*' contains an umlaut and is here transcribed to *M. gruendeli*.

Scissurella evaensis Bandel, 1998, suggests with the suffix '-ensis' a name given for the geographic provenance; however, Bandel (1998) was explicit in naming the species for Mrs Eva Vinx. Accordingly, the proper formation of the name would have been 'evaee'. The original spelling is maintained and treated as a noun in apposition.

In the family Scissurellidae, species epithets that result in identical epithets being found in two scissurellid species are encountered; on occasion, gender agreement may produce a minor difference. These pairs are '*Daizona pacifica*' Bandel, 1998 and *Sinezona pacifica* (Oliver, 1915) (cf. Marshall 2002); *An. indonesia* Bandel, 1998 and *Sukashitrochus indonesicus* Bandel, 1998; *Larochea miranda* Finlay, 1927 and *Suk. mirandus* (A. Adams, 1862); *An. s.l. tabulata* (Barnard, 1964) and *Satondella tabulata* (Watson, 1886); *Th. reticulata* Bandel, 1998 and *Sci. reticulata* Philippi, 1853; *Trogoconcha marshalli* (Lozouet, 1998) and *Sci. marshalli* Bandel, 1998; *Sin. depressa* (Watson, 1897) and *Sci. depressa* Reuss, 1860; *Scissurella plicata* Philippi, 1836 and *Sin. plicata* (Hedley, 1899) (= *Sci. laevigata* d'Orbigny, 1824). All these species pairs are found in discrete genera; hence, secondary homonymy is ruled out.

Significant single letter differences in species epithes are: *Sci laevigata* d'Orbigny, 1824 and *Sin. levigata* (Iredale, 1908); *An. alta* (Watson, 1886) and *Sci. alto* n. sp.

Family SCISSIONELLIDAE Gray, 1827

Description

Shell small (<6 mm), trochiform (*Anatoma*, *Thieleella*, *Satondella*), naticiform (*Scissurella*, *Sinezona*, *Ariella*, *Larochea*, *Larocheopsis*, *Troglonconcha*), neritiform (*Incisura*, *Larochea*, *Temnocinclus*, *Temnozaga*), haliotiform (*Incisura*), calyptrotaeiform (*Depressizona* n. gen.). Protoconch 1/2 to 1 whorl, sculpture variable: smooth, reticulate (*Thieleella*), spirals, axials, flocculent, pitted (*Sutilizona*); apertural varix present or absent; apertural margin convex or sinusoid. Sculpture variable: smooth, axials, spirals, folds. Usually with selenizone and slit or single foramen; also without selenizone, and/or without foramen or slit (*Coronadoa*, *Larochea*, *Larocheopsis*, *Troglonconcha*). Anomphalous or umbilicate. Nacre inconspicuous. Coiled operculum with central nucleus usually present (absent in *Larochea*, *Larocheopsis*).

Radula rhipidoglossate, rachidian serrated, three to five serrated laterals, last lateral usually enlarged, marginals serrated. Two shell muscles or fused horseshoe-shaped muscle. Epipodial and cephalic tentacles with or without papillae. Eyes usually present (absent in *Temnocinclus*, *Temnozaga*, *Sutilizona*). Gills paired or single, monopectinate or bipectinate, with bursicles; hypobranchial gland present.

Subfamily SCISSIONELLINAE Gray, 1847

Type genus: *Scissurella* d'Orbigny, 1824.

Other genera: *Incisura* Hedley, 1904; *Sinezona* Finlay, 1926; *Coronadoa* Bartsch, 1946; *Sukashitrochus* Habe & Kosuge, 1964; *Ariella* Bandel, 1998; *Satondella* Bandel, 1998.

Description

Shell small (<3 mm), trochiform (*Coronadoa*, *Scissurella*), naticiform (*Satondella*, *Scissurella*, *Sinezona*, *Ariella*), neritiform and haliotiform (*Incisura*). Protoconch sculpture variable: smooth, spirals, axials, flocculent; apertural varix present or absent; apertural margin convex or sinusoid. Sculpture variable: smooth, axials, spirals, folds. Brood pouch absent. Usually with selenizone (no selenizone in *Ariella*), selenizone on shoulder, with slit or single foramen. Usually umbilicate. Operculum coiled with central nucleus.

Rachidian serrated, five serrated laterals, first through third laterals similar, fourth lateral reduced, fifth lateral enlarged, broadened, asymmetrically serrated. Two shell muscles or fused horseshoe-shaped muscle. Epipodial and cephalic tentacles with papillae. Eyes present.

Differential diagnosis

Anatominae have the slit and selenizone at the periphery and *Thieleella* shows reticulate sculpture on the protoconch. Temnocinclinae have a planispiral shell with extremely increased expansion rate of the whorl, a radula with three laterals and are found exclusively at hydrothermal vents. Sutilizoninae have a pitted protoconch, a radula with three to four laterals, a combination of highly sculptured and depressed shell and are exclusively found at hydrothermal vents. Larocheinae lack any sign of selenizone, slit or foramen and, in contrast with the scissionelline *Coronadoa*, do not have protoconch sculpture with axials. Depressizoninae n. subfam. have a calyptrotaeiform shell.

Genus *Scissurella* d'Orbigny, 1824

Scissurella d'Orbigny, 1824: 343. Type species *Scissurella laevigata* (SD: Gray, 1847) (possibly a synonym of *Scissurella costata* d'Orbigny, 1824; cf. Marshall 2002).

Schismope Jeffreys, 1856: 321. Type species 'Scissurella striatula' Philippi, 1844 (M) (misidentified; cf. Marshall 2002).

Woodwardia Crosse & Fischer, 1861: 160. Type species 'Scissurella elegans' d'Orbigny, 1824 (M) (misidentified; cf. Marshall 2002).

Maxwellella Bandel, 1998: 19. Type species *Scissurella annulata* Ravn, 1933 (OD, †).

Reussella Bandel, 1998: 44. Type species *Scissurella depressa* Reuss, 1860 (OD, †).

Praescissurella Lozouet, 1998: 66. Type species: *Scissurella depontaillieri* Cossmann, 1879 (OD, †).

Description

Shell trochiform, shoulder rounded or angular. Sculpture usually reticulate, but also with predominating axials or axials only; no spiral keel(s) on base. Slit open, selenizone on shoulder, starting at less than 3/4 whorls of teleoconch I, with moderately elevated keels. Protoconch with variable sculpture: smooth, spirals, fine axials, strong axials; varix absent or present, if present restricted to aperture, or connecting to embryonic cap; aperture sinusoid or simple convex curve. Umbilicus usually open, with or without carina, some with funiculus; rarely anomphalous. Operculate. Radula n-5-R, fifth lateral broadly enlarged, asymmetrically serrated. Anatomy essentially unknown.

Differential diagnosis

In *Sinezona*, the slit is always closed anteriorly to form a foramen; juvenile *Sinezona* may be difficult to distinguish from *Scissurella*. Half the *Scissurella* species can be distinguished by the presence of a carina or a funiculus in the umbilical region. Fully grown specimens can often be identified by the marked drop of the final quarter whorl along the axis of the shell. *Sukashitrochus* has prominent spiral keel(s) on the base, the umbilicus is always bordered by a carina and the slit is closed anteriorly to form a foramen (see above). *Ariella* only shows a foramen and lacks a selenizone. *Coronadoa* lacks a selenizone, slit or foramen. *Incisura* usually has a very smooth shell and is rather neritiform than trochiform.

Remarks

Marshall (2002) discussed the nomenclatorial problems associated with *Schismope* and *Woodwardia* and his suggestion of maintaining prevalent usage of the taxa and, hence, synonymising both generic names under *Scissurella* is followed here.

Among the trochospiral scissurellids with an open slit, Bandel (1998) diagnosed *Maxwellella* as containing those species with a depressed apex, as opposed to the low trochospiral apex in *Scissurella*. Although the species assigned by Bandel to *Maxwellella* all show a more or less depressed apex, the same condition is found in several species retained by Bandel in *Scissurella* (e.g. *Sci. marshalli* Bandel, 1998, *Sci. rota* Yaron, 1983 and *Sci. eocaenica* Bandel, 1998). Furthermore, some species assigned to *Maxwellella* show a hardly depressed apex with an overall trochiform shell (e.g. 'M.' *unispirata*), which are difficult to separate from species placed in other genera (e.g. *Sci. evensis*). The elevation or depression of the apex in scissurellids with an open slit exhibits a continuous gradation, with no apparent separation of conditions. Accordingly, *Maxwellella* is synonymised here under *Scissurella*.

Some of the fossil members of *Maxwellella*, including the type species, are unique in that the top margins of all whorls are higher than the tip of the protoconch. It may be possible to retain the genus *Maxwellella* for those species using a much restricted generic

concept (e.g. Schnetler *et al.* 2001), but too little material is available to make an informed decision. There are no covariant characteristics that could support a separation of those species. No Recent scissurellid species are known that show this condition.

Maxwelletta unispirata Bandel, 1998 is remarkably similar to *Scissurella evaensis* Bandel, 1998 and both are from Satonda, Indonesia. They share a protoconch with fine axials and an apertural varix, a shell sculpture dominated by strong axials, in between which finer irregular axials are found, and a row of raised tubercles on the strong axials on the shoulder and the base. The only difference is that, in *M. unispirata*, the apparent position of the body whorl with respect to the remainder of the spire is somewhat lower. However, the angle at which the SEM were taken also differs and can account for this apparent difference. I here synonymise *M. unispirata* (described in Bandel 1998: 22) under *Sci. evaensis* (described in Bandel 1998: 15). Additional specimens to those examined by dissecting microscope and SEM from Okinawa (15 lots), Indonesia (one lot), Thailand (two lots), Papua New Guinea (two lots), Philippines (two lots) and the Solomon Islands (one lot) in the LACM collection confirm the above assessment.

Reussella was diagnosed by the rounded shoulder, which is flat in *Scissurella* and *Maxwelletta* (Bandel 1998). The type species of the genera show such a distinction, yet the scissurellid species cannot be assigned unambiguously to either of these two morphs due to extensive intergradation among species. The assignment of species to the genera in question by Bandel (1998) according to his own criteria is also inconsistent. *Scissurella cossmanni* Depontaillier, 1881 and *Sci. reticulata* Philippi, 1853 are close to identical in apertural profile to '*R.*' *depressa* (Reuss, 1860) (non Watson, 1897) or '*R.*' *plicata* (Hedley, 1899). Furthermore, Bandel (1998) diagnosed *Reussella* with an open slit to separate it from those genera with a foramen, yet '*R.*' *plicata* (Bandel 1998: pl. 15, fig. 8, pl. 16, fig. 1) has a closed slit and a foramen. Because the generic concept of *Reussella* lacks discrete diagnostic characteristics and cannot be made more precise, the genus is here synonymised under *Scissurella*.

Praescissurella was introduced for the fossil *Sci. depontaillieri* Cossmann, 1879 based on the presence of a funiculus in the umbilicus. This characteristic does not seem to diagnose a particular group, but is homoplastic. Schnetler *et al.* (2001: 84) found it difficult to assign their '*Praescissurella* ? *ravni*' Schnetler, Lozouet & Pacaud, 2001 to this genus with sufficient certainty, despite relatively well-preserved material, further questioning the validity of this genus. *Praescissurella* is here synonymised under *Scissurella*.

Scissurella alto n. sp.

(Figs 1–2)

Scissurella sp.: Raines, 2002

Material examined

Holotype. LACM 2914

Paratypes. LACM 2915, gold coated on SEM stub; paratype AMS C.205034; two paratypes ANSP 410309; two paratypes UMT RM28240, RM28241; two paratypes BMNH 20020267.

Type locality. Off Punta Rosalia, east of Anakena, Easter Island, 10–20 m, in sand and rubble at base of cliff, Dec. 2000. Leg. B. Raines.

Description

Shell medium size (1.07 mm holotype; 1.09 mm paratype), globular, 1.08- (holotype) and 1.25-fold (paratype) wider than high. Colour off-white. Teleoconch II with almost flat

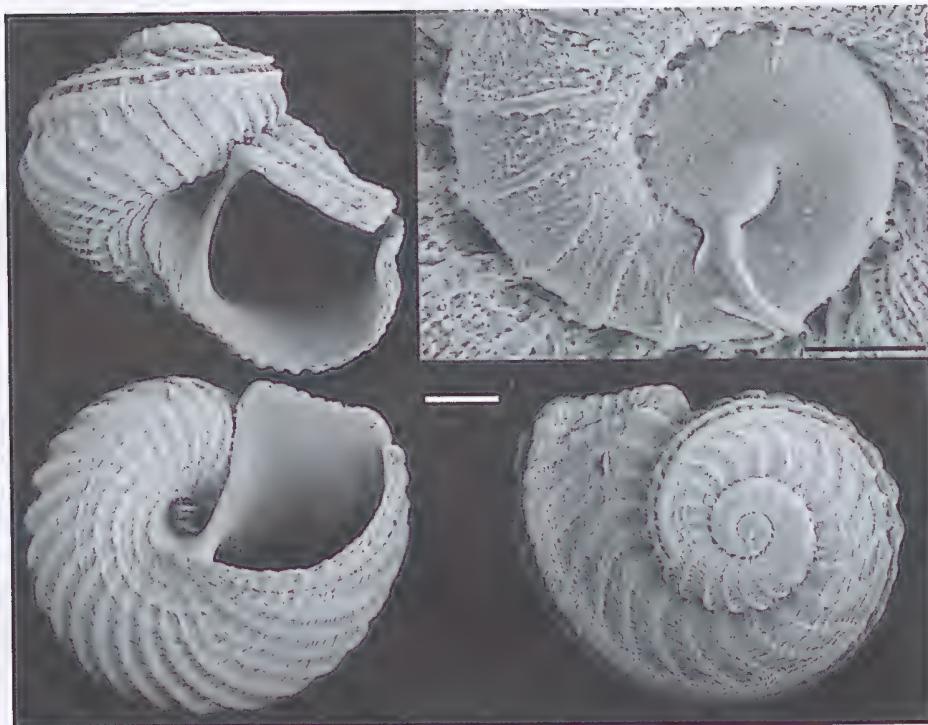


Fig. 1. *Scissurella alto* n. sp., holotype LACM 2914. Scale bars: shells 200 μm ; protoconch 50 μm .

shoulder. Selenizone above widest part of shell. Distinct groove below selenizone, base rounded. Axials predominate, 19 on last whorl. Three to five irregular fine spirals on shoulder, approximately 15 on base, running threadlike over axials. Umbilicus narrow, open, with strong keel at margin, inner wall smooth. Aperture rotund, adumbilical portion thickened at suture and at intersection with umbilical keel, giving square appearance of adumbilical portion of aperture. Teleoconch I $1\frac{1}{4}$ whorls, sculpture early on without spirals but with flocculations, after one whorl spirals appear. Selenizone with low, sturdy, blunt keel, growth increments coincide exactly with axials on teleoconch II. Slit open, margins parallel at aperture. Protoconch 134 μm (holotype), 140 μm (paratype), slightly sunken in, smooth, with strong subterminal varix connecting to embryonic cap, aperture sinusoid. Animal unknown.

Distribution

Easter Island.

Differential diagnoses

Scissurella koeneni Semper, 1865, from the Philippines and Indonesia, has weaker and more numerous axials (47 in *Sci. koeneni*, 19 in *Sci. alto* n. sp.), has a teleoconch of only 1 to 1 whorls, the keel of the selenizone is fine, has a sharp edge, the growth increments do not align with the axials of teleoconch II and the protoconch has strong axials (Thiele 1912; Bandel 1998). *Scissurella hoernesii* Semper, 1865, from the Philippines and Indonesia, has weaker and more numerous axials (25 in *Sci. hoernesii*, 19 in *Sci. alto* n. sp.) and more

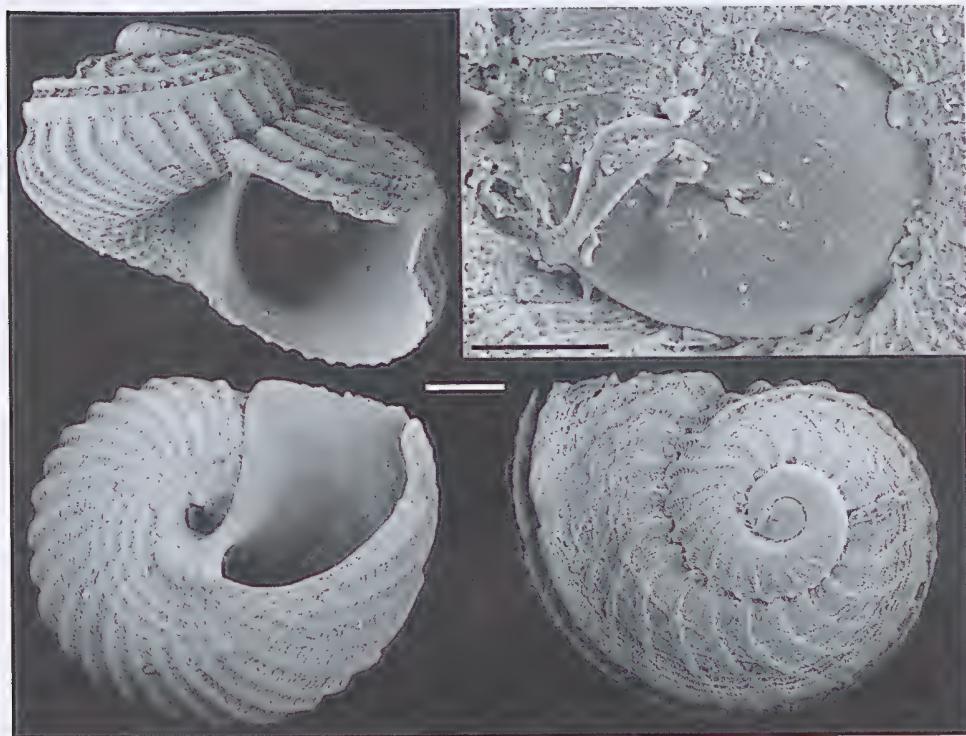


Fig. 2. *Sinezona alto* n. sp., paratype LACM 2915. Scale bars: shells 200 µm; protoconch 50 µm.

numerous spirals on the shoulder (11 in *Sci. hoernesi*, three to five in *Sci. alto* n. sp.), teleoconch I has 1 whorls (1½ in *Sci. alto* n. sp.) and the keel of the selenizone is fine, has a sharp edge and the growth increments do not align with the axials of teleoconch II (Thiele 1912; Bandel 1998).

Etymology

The species honours the developers of the first desktop computer, the *Alto* (cf. Hiltzik 1999). This invention made modern phylogenetic analysis possible. Noun in apposition.

Genus *Satondella* Bandel, 1998

Satondella Bandel, 1998: 64–65. Type species: *Satondella minuta* Bandel, 1998 (OD).

Description

Shell small, early whorls more or less planispiral, last 1/4 whorl dipping markedly. Protoconch smooth or with spiral sculpture, apertural varix absent. Axials predominant, spirals much weaker. Umbilicus open. Selenizone with strong keels, terminally elevated forming chimney at anterior margin of foramen.

Differential diagnosis

Satondella is characterised by the more or less planispiral shell in conjunction with the smooth or spirally sculptured apex lacking a terminal varix. *Scissurella* has an open slit, is often markedly trochospiral and the protoconch shows an apertural varix. *Sinezona* shares

the foramen with *Satondella*, but shows an apertural varix of the protoconch as well. *Sinezona cyprina* is similar in overall shell morphology, but the protoconch sculpture and the presence of an apertural varix on the protoconch separates it from species in *Satondella*. *Sukashitrochus* has prominent keels on the base of the shell (Fig. 15*I*) and has a more elevated spire. *Coronadoa* lacks a selenizone, slit or foramen (Fig. 16*D*). *Incisura* usually has a smooth sculpture and has either a higher spire in the naticiform *I. rosea* or is neritiform as in *I. lytteltonensis* (Fig. 10).

Remarks

Satondella tabulata (Watson, 1886) and a fourth, undescribed species from Queensland are assigned to this genus. Redfern (2001) showed an interesting specimen as ‘*Sin. tabulata*’ (Watson, 1886). The specimen has a foramen with elevated keels, but has a much more elevated spire. Whether this specimen actually represents Watson’s species is unclear.

Satondella senni n. sp.

(Fig. 3)

Satondella sp.: Raines, 2002

Material examined

Holotype. LACM 2911.

Paratypes. LACM 2923, gold coated and mounted on SEM stub; paratype AMS C..205032; paratype ANSP 410307; paratype UMUT RM28238; paratype BMNH 20020265.

Type locality. Off Punta Rosalia, east of Anakena, Easter Island, 10–20 m, in sand and rubble at base of cliff, Dec. 2000. Leg. B. Raines.

Description

Shell small (1.08 mm), 1.5-fold wider than high. Colour off-white. Teleoconch II with only slightly concave to almost flat shoulder. Selenizone at approximate 45° angle to shell axis, inside of widest part of shell, strongly keeled. Suture at widest point of earlier whorl, descending in part closest to aperture. Shoulder with approximately six fine but distinct spiral cords, first spiral with onset of selenizone; spirals intersected by broad but less distinct curved axial cords, 13 on last half whorl, first axial immediately after protoconch on teleoconch I. Side of shell with sculpture similar to that on shoulder. On base, strength of axials and spirals reversed. Umbilicus wide, open, bordered by strong edge, interior surface straight and smooth. Aperture subrectangular, obtuse angle at inner base, adumbilical margin thickened, upper lip strongly overhanging. Protoconch 142 µm, 3/4 of a whorl, in one plane with top of shell, aperture sinusoid, no subterminal varix. Embryonic cap smooth, early protoconch with irregular granulation, last half whorl with three faint but distinct spiral cords on smooth surface. Animal unknown.

Distribution

Easter Island.

Differential diagnoses

Satondella minuta Bandel, 1998, from Indonesia, has a depressed protoconch, whereas in *Sat. senni* n. sp., the protoconch is in the same plane as the first teleoconch whorl. The protoconch of *Sat. minuta* is smooth, whereas *Sat. senni* has the unique spiral sculpture.



Fig. 3. *Satondella senni* n. sp., holotype LACM 2911. Scale bars: shells 200 µm; protoconch 50 µm.

Satondella minuta has a stronger keel of the selenizone and fewer and stronger axials on the teleoconch. In *Sat. minuta*, the suture is deep and the inner walls of the whorls are rounded, whereas in *Sat. senni* the suture is very shallow and the inner wall of the whorl is at a strong angle between the roof of the whorl and the inner side wall. *Satondella tabulata* (Watson, 1886) (not *An. s.l. tabulata* (Barnard, 1964)), according to Watson (1886) and Thiele (1912: figure copied from Watson 1886), from Isla de Culebra, Puerto Rico, is distinguished from *Sat. senni* n. sp. by the rounder hole, a keel in the umbilicus and the bottom adumbilical part of the aperture being rounded as opposed to angular, as in *Sat. senni* n. sp. In addition, the adumbilical part of the aperture shows a narrow shield (absent in *Sat. senni* n. sp.); this condition may be gender related; for discussion, see below. The condition of the protoconch is unknown for *Sat. tabulata*.

Remarks

The protoconch sculpture of *Sat. senni* n. sp. is unique among the known types. It is closest to the single spiral found on fresh specimens of *Sin. plicata* (AMS C334062: Coral Sea; AMS C028241: Tuamotu; AMS C379083: QLD; AMS C379418: Vanuatu; AMS C380658: Society Islands); Bandel's (1998: pl. 16, fig. 2) illustration of *Sin. plicata* shows a slightly eroded protoconch that looks smooth.

Etymology

The species honours my mentor David G. Senn, University of Basel, Switzerland, for his varied introduction to marine biology and for instilling a holistic approach to scientific inquiry.

Genus *Sinezona* Finlay, 1926

Sinezona Finlay, 1926: 341. Type species: *Schismope brevis* Hedley, 1904 (OD).

Schismope auct., not Jeffreys, 1856. Misidentified type species: cf. Marshall 2002.

Woodwardia auct., not Crosse & Fischer, 1861. Misidentified type species: cf. Marshall 2002.

Daizona Bandel, 1998: 57. Type species: *Sinezona doliolum* Herbert, 1986 (OD).

Description

Shell small (<3 mm), trochoid. Protoconch usually with strong axials; spirally sculptured and smooth ones also known. Protoconch varix present with or without contact to embryonic cap. Anomphalous or umbilical wall forming continuous curve with base of shell, without carina or funiculus. Sculpture usually with axials predominating over spirals, no spiral keel(s) on base. Selenizone on shoulder, slit closed anteriorly forming foramen, keels of selenizone and foramen of more than 1/4 up to the full width of the selenizone.

Differential diagnosis

Sukashitrochus shares the anteriorly closed foramen, but has prominent spiral keel(s) on the base and the umbilicus is always bordered by a carina. *Scissurella* never closes the slit anteriorly. Juvenile *Sinezona* may be difficult to distinguish from *Scissurella*. Half the *Scissurella* species can be distinguished by the presence of a carina or a funiculus in the umbilical region. Fully grown specimens can often be identified by the marked drop of the final quarter whorl along the axis of the shell. *Ariella* shares the foramen with *Sinezona*, but lacks a selenizone. *Coronadoa* lacks a selenizone, slit or foramen (Fig. 16D). *Incisura* usually has a smooth sculpture and has either a higher spire in the naticiform *I. rosea* or is neritiform, as in *I. lytteltonensis* (Fig. 10).

Remarks

The only diagnostic character is the presence of a selenizone in conjunction with the slit closing anteriorly to form a foramen. The protoconch sculpture usually consists of strong axials; however, this condition is not restricted to *Sinezona* but also applies to half the species of *Scissurella*. Accordingly, protoconch sculpture is not a diagnostic characteristic for *Sinezona*. Burnay and Rolán (1990) based their generic assignment of '*Sinezona*' *lobini* on protoconch sculpture, although no specimen with a slit closed into a foramen could be found. Given the non-diagnostic nature of protoconch sculpture and the consistently open slit, the species is reassigned to *Scissurella*.

Daizona was diagnosed by Bandel (1998) based on the length of the selenizone. Marshall (2002) recently synonymized *Daizona* under *Sinezona* and I independently arrived at the same conclusion. A histogram of angles of protoconch to selenizone and angle of selenizone for all 14 species with sufficiently clear illustrations (*Sin. marshalli* did not show the separation of selenizone from foramen) are shown in Fig. 4. Measurements were taken to the nearest 5°. There are no discernable groupings in the plot, showing that any separation of taxa based on this characteristic is arbitrary and indefensible. Statistical testing for deviation from normal distribution (alternative hypothesis: bimodal distribution) and rectangular distribution (null hypothesis: all values with equal frequency) was performed with the Kruskal–Wallis test for categorised data, Lilliefors test for continuous data and chi-squared test. All tests for both variables and either distribution were insignificant. *Daizona* is synonymised under *Sinezona*.

Interesting patterns emerged from the correlation coefficients between the selenizone and foramen (Table 1). Besides the two metrics introduced above, the angular measurement

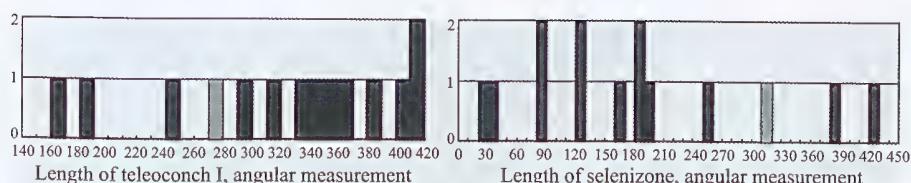


Fig. 4. Histogram of two shell morphometric parameters in *Sinezona*: *Sin. beddomei*, *Sin. brevis*, *Sin. cingulata*, *Sin. confusa*, *Sin. crossei*, *Sin. doliolum*, *Sin. ferriezi*, *Sin. insignis*, *Sin. iota*, *Sin. levigata*, *Sin. pacifica*, *Sin. plicata*, *Sin. semicostata*, *Sin. zimmeri* n. sp. The type species of *Daizona*, *Sin. doliolum*, is highlighted in grey. Left, length of teleoconch I, as angular measurement. Right, angular measurement of length of selenizone. All measurements were taken to the nearest 5°. Distributions are not significantly different from either normal or rectangular distribution.

Table 1. Correlation coefficients for three selenizone- and foramen-related metrics for 14 *Sinezona* species

Top right quadrant: alpha-error probability of parametric correlation coefficient; bottom left quadrant: alpha-error probability of Spearman rank correlation coefficient

	Teleoconch I	Selenizone	Foramen
Teleoconch I	—	0.31	0.048
Selenizone	0.38	—	0.0011
Foramen	0.072	0.00046	—

Teleoconch I, angular measurement from aperture of protoconch to beginning of selenizone; selenizone, angular measurement of selenizone length; foramen, angular measurement of foramen length.

of the length of the foramen were also obtained. Because these measurements were taken to the nearest 5°, both the parametric Pearson product-moment correlation coefficient and the non-parametric Spearman rank correlation coefficient for ordinal data were calculated. There is no correlation between the onset of the selenizone and the length of the selenizone and the correlation between onset of the selenizone and the foramen is marginally significant. However, there is a significant correlation between the length of the selenizone and the foramen. It is unclear whether this correlation has any underlying biological significance, but it is not correlated to size ($0.36 < P < 0.77$).

Sinezona zimmeri n. sp.

(Figs 5–9)

Material examined

Holotype. LACM 2912.

Paratypes. 1–3 LACM 2913: gold coated on SEM stub; paratypes 4 and 5 AMS C.404165, AMS malacology SEM stub 4370, 10th and 11th specimen counterclockwise from top mark, approximately 6 o'clock, paratype 6 AMS C.406377, AMS malacology SEM stub 4394, eighth specimen counterclockwise from top mark; paratype AMS C.205033; two paratypes ANSP 410308; paratype UMUT RM28239; paratype BMNH 20020266; paratype 7 AMNH 301625, Yuko Haoa Avaka, Akahanga, Easter Island, Aug. 20 1998.

Type locality. Off Punta Rosalia, east of Anakena, Easter Island, 10–20 m, in sand and rubble at base of cliff, Dec. 2000. Leg. B. Raines.

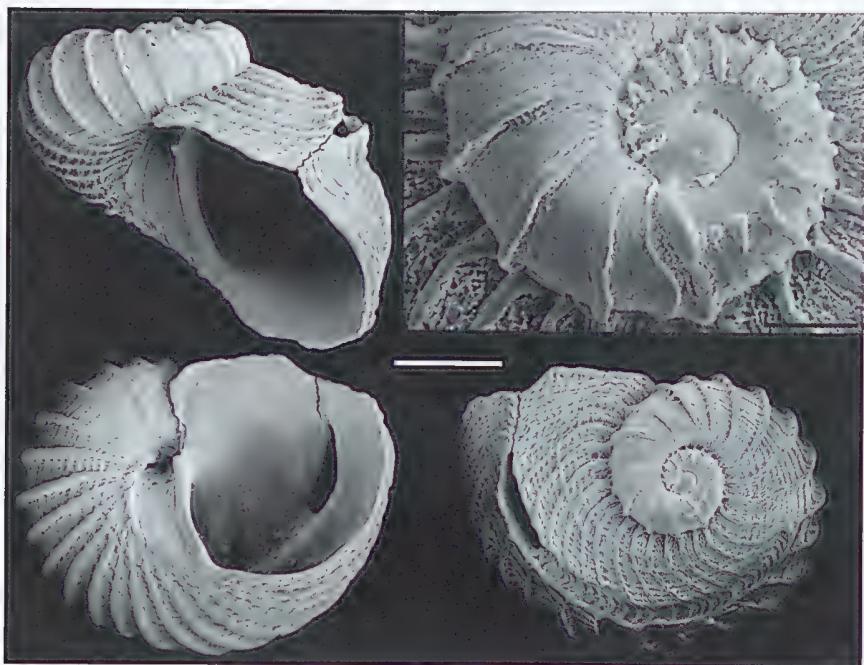


Fig. 5. *Sinezona zimmeri* n. sp., holotype LACM 2912. Scale bars: shells 200 µm; protoconch 50 µm.

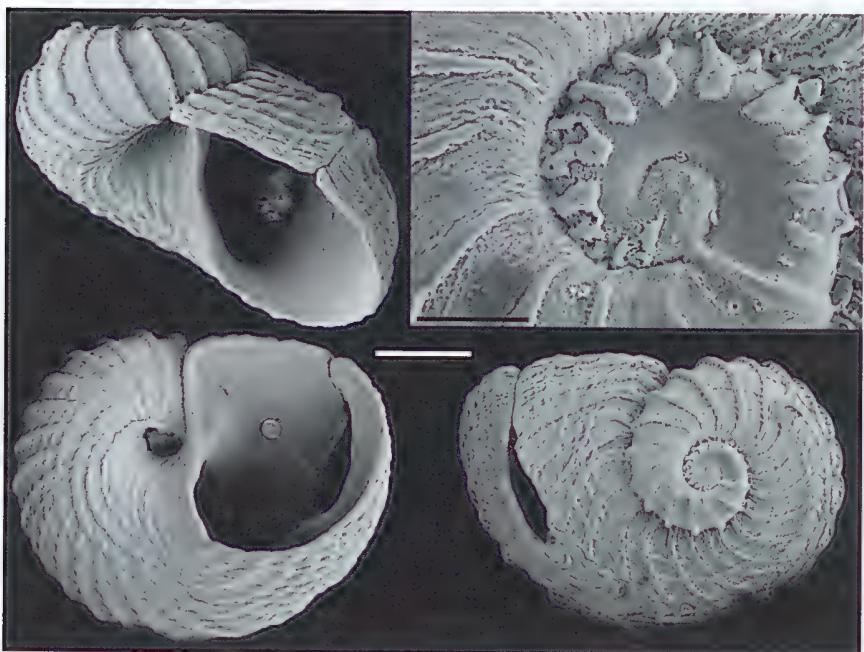


Fig. 6. *Sinezona zimmeri* n. sp., paratype 1 LACM 2913. Scale bars: shells 200 µm; protoconch 50 µm.



Fig. 7. *Sinezona zimmeri* n. sp., paratype 2 LACM 2913. Scale bars: shells 200 µm; protoconch 50 µm.

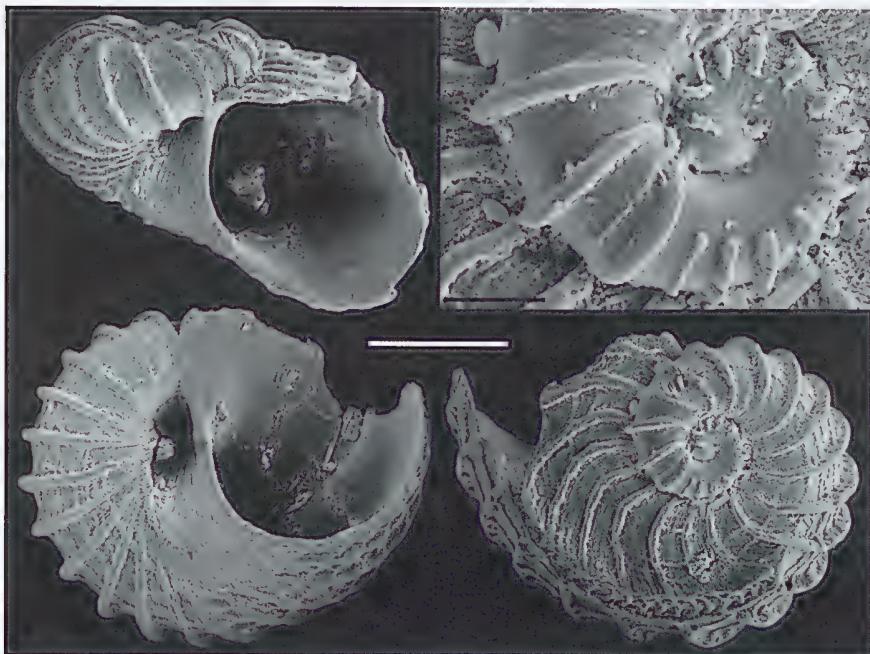


Fig. 8. *Sinezona zimmeri* n. sp., paratype 3 LACM 2913. Scale bars: shells 200 µm; protoconch 50 µm.

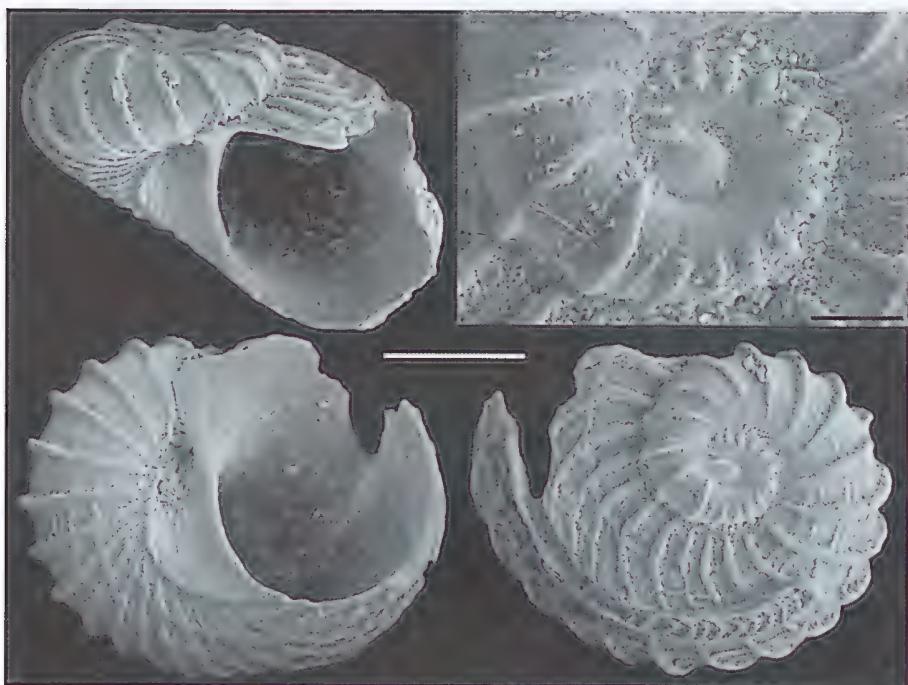


Fig. 9. *Sinezona zimmeri* n. sp., paratype (AMS no. 3504, Anakena Beach, Easter Island). Scale bars: shells 200 μm ; protoconch 50 μm .

Description

Shell small (holotype: 0.675 mm, paratypes 0.579–0.826 mm; mean \pm SD = 0.697 \pm 0.103 mm), globular (width/height 1.12 in holotype, mean \pm SD = 1.38 \pm 0.384). Colour off-white. Teleoconch I of 3/4 to 7/8 whorl. Teleoconch II of approximately 2/3 whorl with flat to slightly convex shoulder. Selenizone above widest part of shell, closed anteriorly in mature specimens; growth marks distinct, more numerous than and not coordinated with axials of whorl; keel low, often eroded in earlier portion. Foramen elongate-lanceolate, rounded posteriorly, pointed anteriorly. Suture at widest point of previous whorl, descending with growth of shell. Shell with 17–25 axial ribs (21 in holotype) on body whorl, intersected by finer spirals forming only weak knots at intersection. Spirals appear ontogenetically progressively from base to suture. Umbilicus open, funnel like, bordered by weak edge, interior surface straight, smooth. Aperture subrectangular, obtuse angle at inner base, upper lip strongly overhanging. Protoconch 150 μm (holotype): mean \pm SD = 152 \pm 4.96 μm , one whorl. Embryonic cap smooth or irregularly sculptured. Remainder with strong, broad axials from just inside of highest point of whorl towards periphery, otherwise smooth. Axials approximately 12, may bifurcate towards periphery. Subterminal varix strong, connecting to embryonic cap only in some specimens. Aperture usually round, in some specimens weakly sinusoid. Animal unknown.

Distribution

Easter Island.

Differential diagnosis

Scissurella koeneni from the Indo-Pacific has a an open slit even after a full whorl of teleoconch II, whereas in *Sin. zimmeri* n. sp. the slit is closed, forming a foramen after less than half a whorl from the start of the selenizone. In *Sin. zimmeri* n. sp., the axials are stronger, the keels bordering the selenizone are lower and the sculpture of the protoconch consists of strong axials, as opposed to the fine irregular axials of *Sci. koeneni*. *Sinezona pacifica* (Oliver, 1915) (non Bandel, 1998) from southern Australia and New Zealand has spiral sculpture on the base that is in the form of slightly sloping steps, as opposed to the raised cords of *Sin. zimmeri* n. sp. The *Scissurella rota* from East Africa has a protoconch with fine irregular axials, as opposed to the strong axials of *Sin. zimmeri* n. sp. In *Sci. rota*, the slit remains open after over a full teleoconch II whorl and the sculpture includes pointed processes at the intersection of spirals and axials. *Scissurella staminea* (A. Adams, 1862) from Japan has a spiral sculpture on the base that is in the form of slightly sloping steps, as opposed to the raised cords of *Sin. zimmeri* n. sp. and the slit remains open over a full whorl after the start of the selenizone. *Scissurella evaensis* (Bandel, 1998) from the Indo-Pacific lacks spiral sculpture and has a protoconch with fine irregular axials, as opposed to the strong axials of *Sin. zimmeri* n. sp.

Etymology

The species honours my advisor, mentor and friend Russel L. Zimmer, University of Southern California, Los Angeles, USA, in appreciation of his generous support as well as for his significant contributions to invertebrate zoology.

Incisura Hedley, 1904

(Fig. 10)

Incisura Hedley, 1904: 17–19. Type species: *Scissurella lytteltonensis* Smith, 1894 (M).

Scissurona Iredale, 1924: 215–216. Type species: *Scissurella rosea* Hedley, 1904 (OD).

Description

Shell naticiform to haliotiform, shoulder rounded, sculpture smooth or with spirals predominating, no spiral keel(s) on base. Protoconch with strong axials, no varix, aperture rounded convex. Umbilicus with carina or funiculus. Slit open or closed into foramen, selenizone on shoulder, starting at less than $\frac{3}{4}$ teleoconch I whorls, keels very low. Operculate. Radula n-5-R, fifth lateral broadly enlarged, with asymmetrically serrated cusp.

Differential diagnosis

The smooth sculpture and the protoconch with the strong axials distinguishes *Incisura* from any other scissurellid genus. The overall shell shape of *Incisura* and juvenile *Pseudorimula* is striking, particularly between *I. lytteltonensis* and *P. midatlantica* McLean, 1992, as illustrated by Warén and Bouchet (2001). However, the protoconchs are very distinct; *Incisura* has broad axial ribs, whereas in *Pseudorimula* the protoconch shows tight spiral sculpture of an undulating nature that is finely pitted.

Remarks

The traditional distinction between *Incisura* and *Scissurona* is based on the overall shell shape, where, in *Incisura*, with the sole species *I. lytteltonensis*, it is more depressed, as

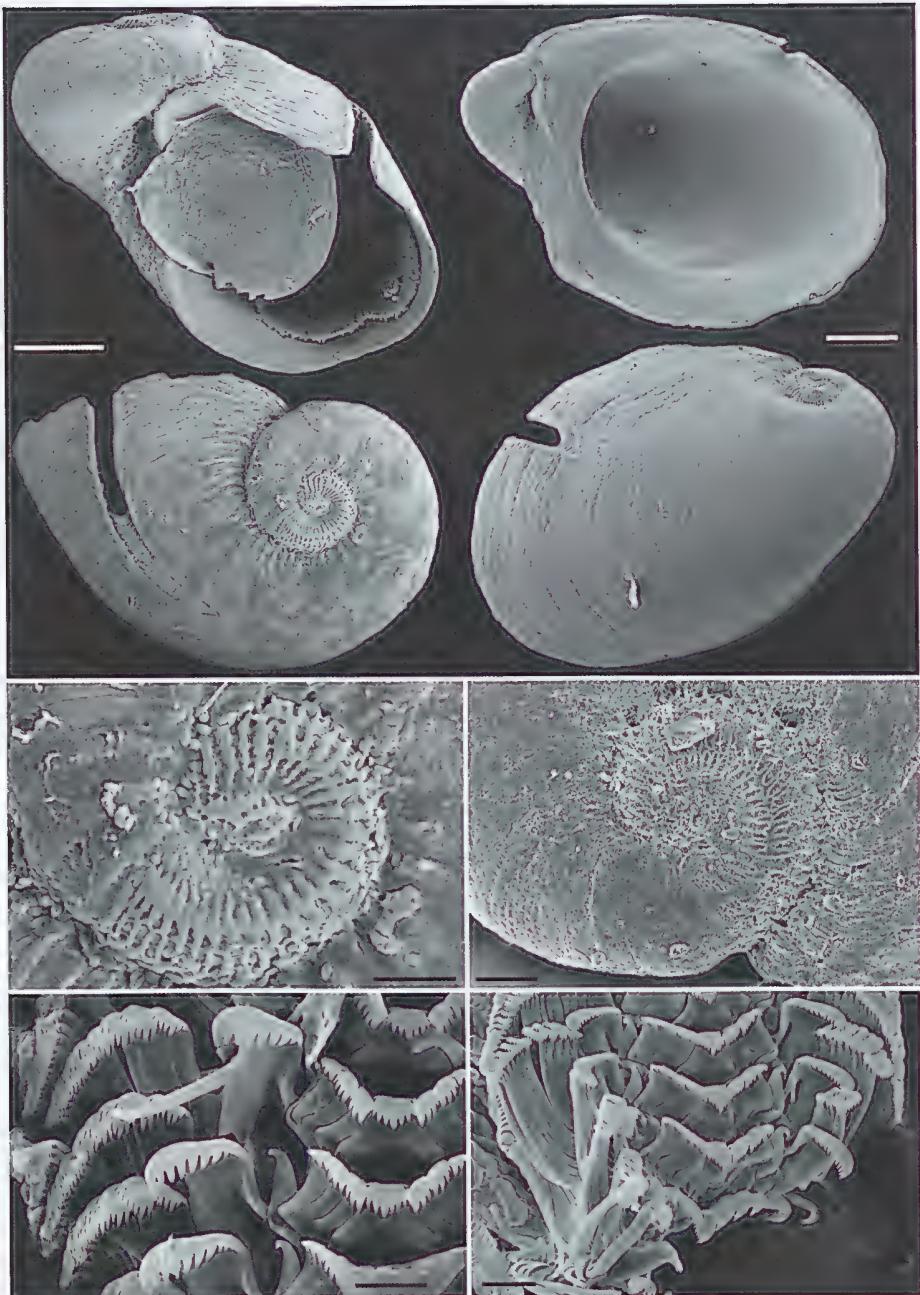


Fig. 10. Left column, *Incisura lytteltonensis*. LACM 87-87: shell; LACM 87-87: radula. Right column, *Incisura ('Scissurona') rosea remota*. AMS C.402700/stub 4363. Western R. Cove, N. coast of Kangaroo: shell. AMS C.402698/stub 4366. On exposed side of Wimbie Beach: radula. Scale bars: shells 200 µm; protoconch 50 µm.

opposed to the three nominal species in *Scissurona* (Bandel 1998); the overall similarity of all species had been noted by some authors (e.g. Hickman 1998; Marshall 2002). The operculum is present in all species (Fig. 10; Bandel 1998), although in *I. lytteltonensis* it has lost its functionality because it can no longer cover the aperture. The radula for *I. lytteltonensis* (Thiele 1912; McLean 1989; Fig. 10) and *I. rosea remota* (Fig. 10) do not show any differences. The rachidian is triangular with a pointed cusp with seven denticles. Second and third lateral teeth are similar with a serrated cusp. Fourth lateral has a single fine point, whereas fifth lateral has a prominent cusp, somewhat broader than the base of the rachidian. The marginals are typical for Vetigastropoda with a finely serrated cusp on a long shaft. I do not think that a simple shell morphological variation warrants generic separation of a single species. Hence, I synonymise *Scissurona* under *Incisura*. Although not treated here in full, the fossil *I. fossilis* (Laws, 1940) also fits into this generic concept. *Scissurella obliqua* Watson, 1886, from the Kerguelen Islands, may also be assigned to *Incisura*. The species has an entirely smooth shell and has a somewhat increased expansion rate of the shell. However, the only illustrations available are those of Watson (1886), copied by Thiele (1912).

Genus *Ariella* Bandel, 1998

Ariella Bandel, 1998: 63. Type species: *Ariella haliotimorpha* Bandel, 1998 (OD).

Description

Shell trochoid to naticiform, shoulder rounded, anomphalous. Sculpture of axialis only or predominantly with axialis, no spiral keels on base. Protoconch with fine or strong axialis, varix present or absent, aperture sinusoid. Foramen present, no selenizone, keels of foramen low. No anatomical data.

Differential diagnosis

The diagnostic characteristic for this genus is the single, round to lenticular, open hole, closed anteriorly, and no sign of a selenizone. This condition was recognised as significant for 'Sin.' *pauperata* already by Marshall (1993).

Remarks

The species composition of *Ariella* is rather uncertain. Marshall (2002) noted differences in protoconch sculpture between the type species, *Ar. haliotimorpha*, and species included by Bandel (1998) in *Ariella* (*Ar. pauperata*, *Ar. subantarctica*, *Ar. campbelli* = *Sin. levigata*). Marshall (2002) placed the latter two species in *Sinezona* and did not consider *Ar. lacuniformis* (Watson, 1886). The latter species is approximately 2 mm in size and does not have a selenizone either (Watson 1886: fig. 8). The illustrations in Watson (1886), copied by Thiele (1912), show a globose shell of low profile, which has fine reticulate sculpture and, most significantly, a foramen but no selenizone. In that respect, *Ar. subantarctica* (Hedley, 1916) resembles *Ar. lacuniformis* and is, hence, tentatively placed in *Ariella*. Given the plasticity of the protoconch sculpture demonstrated here, less emphasis is placed on this characteristic for classification purposes and species lacking a selenizone are tentatively placed in *Ariella*, which is provisionally retained as a genus.

Sukashitrochus Habe & Kosuge, 1964

(Fig. 15I)

Sukashitrochus Habe & Kosuge, 1964: 3. Type species: *Scissurella carinata* A. Adams, 1862 (OD).*Description*

Shell trochiform, with spiral keel(s) on base, shoulder rounded or angular. Shell with foramen, selenizone on shoulder, moderately keeled, usually starting after 0.75 whorls (except *Suk. pulcher*: <0.75 whorls). Umbilicus with carina. Shell sculpture variable: predominant axials, reticulate or predominant spirals. Protoconch sculpture variable: smooth, fine irregular axials, flocculent, protoconch varix present, either not touching embryonic cap or forming a bridge to the embryonic cap, shape of protoconch aperture sinusoid. Radula n-5-R with fifth lateral greatly enlarged, broadened, serration asymmetrical. Operculum present.

Differential diagnosis

Sinezona shares the foramen with *Sukashitrochus*, but lacks the keels on the shell. *Scissurella* has an open slit and lacks the keels on the shell. *Ariella* has an open hole, but lacks the keel and a selenizone.

Remarks

Sukashitrochus has been diagnosed (Herbert 1986) with a smooth protoconch, although Bandel (1998) noted other protoconch sculptures among the species assigned to this genus. This characteristic is shown, here, to be highly variable within the genus. The conjunction of keels on the shells with a closed foramen is diagnostic for *Sukashitrochus*. With one exception, the species included in *Sukashitrochus* by Bandel (1998) are congruent with the present analysis. The specimen illustrated by Bandel (1998: pl. 19, figs 1–3) as ‘*Suk. declinans*’ from Sydney, NSW, is actually *Suk. atkinsoni*. *Scissurella declinans* has an open slit, even in a fully mature shell, a rounded base with no trace of a keel, an umbilicus, the slope of which is continuous with the rounding of the base, and has a more tropical distribution, extending to the south only to Queensland (Watson 1886; Jansen 1999).

Sukashitrochus tasmanicus (Petterd, 1879), *Suk. tricarinatus* (Yaron, 1983), *Suk. armillatus* (Yaron, 1983) and *Suk. mirandus* (A. Adams, 1862) (non Finlay, 1927) are also referred to this genus based on the presence of keels on the base of the shell, although not included in the phylogenetic analysis. The gender of the genus is masculine; hence, some of the specific epithets had to be altered (*pulchra*: *pulcher*; *carinata*: *carinatus*; *armillata*: *armillatus*; *miranda*: *mirandus*).

Sukashitrochus mirandus (A. Adams, 1862) is assigned to the genus based on Adams' description, translated by Thiele (1912), noting particularly ‘basi lineis concentricis instructo’ (at the base provided with concentric lines). Thiele (1912) noted that no specimen could be found in the British Museum and that the specimen had not been illustrated by Adams. Therefore, Thiele's figure has to be treated with caution with respect to the identity of the species, which may have to be treated as a *nomen dubium*.

One species is tentatively referred to *Sukashitrochus*. ‘*Scissurella*’ *dorbignyi* (Audouin, 1826) also shows the strong spiral keels on the base, but has an open slit. The illustration of Yaron (1983) shows a shell in which the apertural portion of the shell does not descend,

which can be taken as a sign of being a juvenile shell. It is quite possible that, in this species, the slit will also close and form a foramen when mature. The illustration of the lectotype (Bouchet and Danrigal 1982: fig. 63), designated by Yaron (1983: 267), shows a slightly constricted slit in the broken and, most likely, immature specimen; the species is tentatively transferred to *Sukashitrochus*.

In contrast, ‘*Suk.*’ *saubadae* Lozouet, 1998, from the Oligocene of France, does not show the spiral band at the base of the shell; hence, it belongs in *Sinezona* rather than *Sukashitrochus*. Although not explicitly stated, the species was most likely placed according to the smooth protoconch. The absence of an umbilical cord also suggests a placement in *Sinezona* rather than in *Sukashitrochus*.

Haszprunar (1988) described heteropod-type swimming in a *Sukashitrochus* species. How widespread this behaviour is in *Sukashitrochus* or in Scissurellidae is unknown.

Genus *Coronadoa* Bartsch, 1946

(Fig. 16D)

Coronadoa Bartsch, 1946: 447–448. Type species: *Coronadoa simonsae* Bartsch, 1946 (OD).

Description

Shell trochoid, shoulder rounded. Sculpture axials only, no spiral keel. Protoconch sculpture of fine axials, no varix. Umbilicate with funiculus. No slit, foramen or selenizone. Operculate. Radula n-5-R, fifth lateral broadened, asymmetrically serrated (Fig. 16D).

Differential diagnosis

The absence of a slit, foramen or selenizone distinguishes *Coronadoa* from all other scissurelline genera. The protoconch sculpture of fine axials separates this genus from all larocheine genera, which share, with *Coronadoa*, the absence of a slit, foramen or selenizone, but have a smooth or flocculent protoconch sculpture. Radular differences further differentiate *Coronadoa* from Larocheinae.

Remarks

Coronadoa is a monotypic genus with sole species *C. simonsae*. Its placement in Scissurellinae is indicated by the protoconch sculpture and the radula. Bartsch (1946) had missed the fourth lateral, using a light microscope. The absence of a slit, foramen or selenizone had been taken as a sign of being juvenile (McLean 1967); however, *C. simonsae* maintains this condition even when fully grown. Juveniles of the sympatric *Sin. rimuloides*, with which it had been synonymised, can be clearly separated from *C. simonsae* (Marshall 2002; J. H. McLean, personal communication; D. L. Geiger, personal observations). Marshall (2002) tentatively synonymised *Coronadoa* under *Sinezona*. I agree with Marshall (2002) that the sole distinguishing characteristic is the lack of a selenizone, slit or foramen. I consider this characteristic significant because it is, most likely, caused by anatomical transformation of the mantle, as is the case in Fissurellidae (McLean and Geiger 1998).

Subfamily ANATOMINAE McLean, 1989

Type genus: *Anatoma* Woodward, 1859.
Other genus: *Thielella* Bandel, 1998.

Description

Shell trochoid, thin, shoulder rounded or angulated. Sculpture variable: axials only, predominantly axials, reticulate; no spiral keel(s) on base. Protoconch sculpture smooth, flocculent, reticulate; varix if present not connecting to embryonic cap; aperture sinusoid or curved convex. Umbilicus without carina or keel, in profile describing smooth curve with base of shell. No brood pouch. Slit open, selenizone at periphery, start of selenizone on teleoconch variable, keels of moderate height. Operculum coiled with central nucleus. Radula n-5-R, fifth lateral little to strongly elongated, but not broadened.

Differential diagnosis

The trochoid brittle shells with the peripheral selenizone and slit, and an umbilicus continuously sloping with the base, distinguish Anatominae from the other subfamilies. Scissurellinae have the selenizone on the shoulder and a radula with the fifth lateral broadened and not elongated. Sutilzoninae and Temnocinclinae have a limpet-shaped shell, have two to four laterals and are found exclusively at hydrothermal vents. Larocheiniae lack a slit, foramen or selenizone. Depresszoninae n. subfam. share the flocculant protoconch sculpture but have a calyptroform shell.

Remarks

McLean (1989) introduced Anatominae for *Anatoma* and *Sukashitrochus*. The inclusion of *Sukashitrochus* in Anatominae has been controversial (Numanami and Okutani 1990; Marshall 1993; Amitov and Zhegallo 1998; Bandel 1998; Lozouet 1998; Sasaki 1998) and the present analysis indicates that *Sukashitrochus* is a member of Scissurellinae. According to McLean (1989), *Sukashitrochus* shares radular similarities with *Anatoma*. However, radular similarities between *Sukashitrochus* and other scissurelline genera are greater. In particular, the greatly broadened and asymmetrically serrated fifth lateral is shared with other scissurelline genera, whereas in the anatomine species studied, the fifth lateral is enlarged by elongation and is more symmetrically serrated.

Bandel (1998) recently introduced two new genera for Scissurellidae: Anatominae. The three genera he recognised are *Anatoma* Woodward, 1859 (type *Sci. crispata* Fleming, 1828), *Hainella* Bandel, 1998 (type *Sci. euglypta* Pelseneer, 1903) and *Thielella* Bandel, 1998 (type *Sci. amoena* Thiele, 1912). The diagnostic characteristics listed by Bandel (1998) are summarised in Table 2.

The distinction between rounded and scalar whorls made by Bandel is difficult to understand given his generic assignments and illustrations. For instance, the rounded, trochiform *Anatoma* s.s. includes compatible species, such as *An. americana* Bandel, 1998, *An. proxima* (Dall, 1927) and *An. alta* (Watson, 1886), but also species that have a very scalar appearance, such as *An. indonesica* Bandel, 1998, *An. jacksoni* (Melville, 1904) and *An. agulhasensis* (Thiele, 1925). Furthermore, *Th. amoena* is almost identical to *An. indonesica*, as illustrated by Bandel (1998), whereas *Th. reticulata* Bandel, 1998, is almost identical to the illustrated *An. alta*. *Hainella philippinica* Bandel, 1998, is intermediate with respect to overall shell shape between *An. indonesica* and *An. proxima* (Dall, 1927) and not unlike *Th. amoena*. With respect to height to width ratio, *Hainella*

Table 2. Diagnostic characters for generic distinction of *Anatoma* s.s., *Hainella* and *Thieleella* (after Bandel 1998)

Character	<i>Anatoma</i> s.s.	<i>Hainella</i>	<i>Thieleella</i>
Whorls	Rounded	Scalar	Scalar
Apical side		Flattened	
Selenizone	Lateral with lamellae	Lateral, peripheral with lamellae as high as wide	Lateral with lamellae
Shell shape	Wider than high	Wider than high	Higher than wide
Protoconch sculpture	Smooth or faint	Granular or smooth	Reticulate

tends to contain shells that are somewhat wider than those in the other two generic concepts of Bandel. However, no discrete boundary can be determined. Accordingly, differences in overall shell shape cannot be recognised and this supposedly diagnostic characteristic is dismissed.

The protoconch sculpture of the two *Thieleella* species (*Th. amoena* and *Th. reticulata*) are unique and well defined. However, there are no differences in protoconch sculpture between *Anatoma* and *Hainella*.

Given the lack of differentiation between *Anatoma* s.s. and *Hainella*, the latter is here synonymised under the former. *Thieleella* is considered distinct based on the reticulate pattern on the protoconch as the sole diagnostic characteristic, which is also supported in the phylogenetic analysis. Species for which the protoconch sculpture is unknown are here classified as *Anatoma* s.l.

Genus *Anatoma* Woodward, 1859

Anatoma Woodward, 1859: 204. Type species: *Scissurella crispata* Fleming, 1828 (M).
(objective) *Schizotrochus* Monterosato, 1877: 416. Type species: *Scissurella crispata* Fleming, 1828 (M).

Hainella Bandel, 1998: 36–37. Type species: *Scissurella euglypta* Pelseneer, 1903 (OD).
not *Anatomus* Montfort, 1810 (Annelida : Polychaeta : Serpulidae. See McLean 1967; Herbert 1986).

Description

Shell large, trochiform. Spire prominent. Slit deep, open. Slit and selenizone at periphery or slightly above; keels usually prominent, at right angle to shell axis. Umbilicus open, often very constricted, no carina. Protoconch smooth or flocculent, varix absent or faint, not forming bridge to nucleus of embryonic shell. Operculate. Radula as for subfamily.

Differential diagnosis

Thieleella has a protoconch with honeycomb pattern, whereas *Anatoma* is either smooth or with flocculant ornamentation. It is virtually impossible to distinguish these two genera using a light microscope.

Remarks

Anatoma cebuana Bandel, 1998 is here reassigned to *Scissurella*. The position of the slit is significantly above the periphery and the keels are not at a right angle to the axis, but

significantly inclined towards the spire. Furthermore, the early whorl is somewhat sunken in, which is not found in *Anatoma*, but is quite characteristic for *Scissurella*. Two specimens from Okinawa (LACM 79–76) have been examined.

Anatoma rainesi n. sp.

(Figs 11, 12)

Anatoma sp.: Raines, 2002

Material examined

Holotype. LACM 2909.

Paratype. LACM 2910, gold coated and mounted on SEM stub; paratype AMS C.205031; paratype ANSP 410306; two paratypes UMUT RM28236, RM28237; three paratypes BMNH 20020264.

Type locality. Off Punta Rosalia, east of Anakena, Easter Island, 10–20 m, in sand and rubble at base of cliff, Dec. 2000. Leg. B. Raines.

Description

Shell medium size (to 1.5 mm wide), 1.3-fold as wide as high. Colour off-white. Whorls of teleoconch II with convex, rounded shoulder and base. Selenizone slightly above periphery, strongly keeled, turned upward at origin. Suture adjacent to lower border of selenizone on early whorls, somewhat below in later whorls: two to three spiral cords between lower

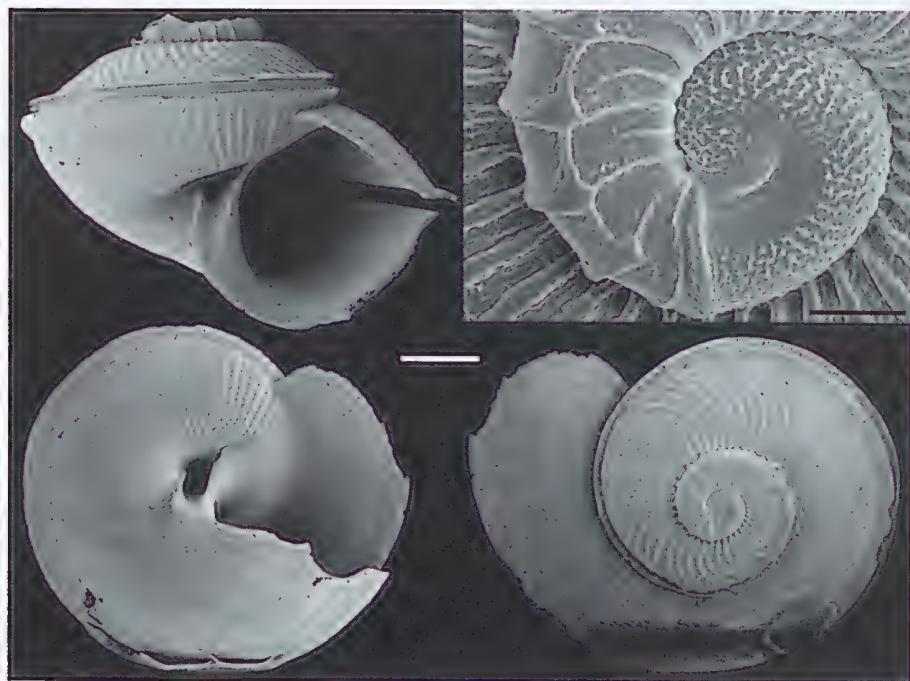


Fig. 11. *Anatoma rainesi* n. sp., holotype LACM 2909. Scale bars: shells 200 µm; protoconch 50 µm.

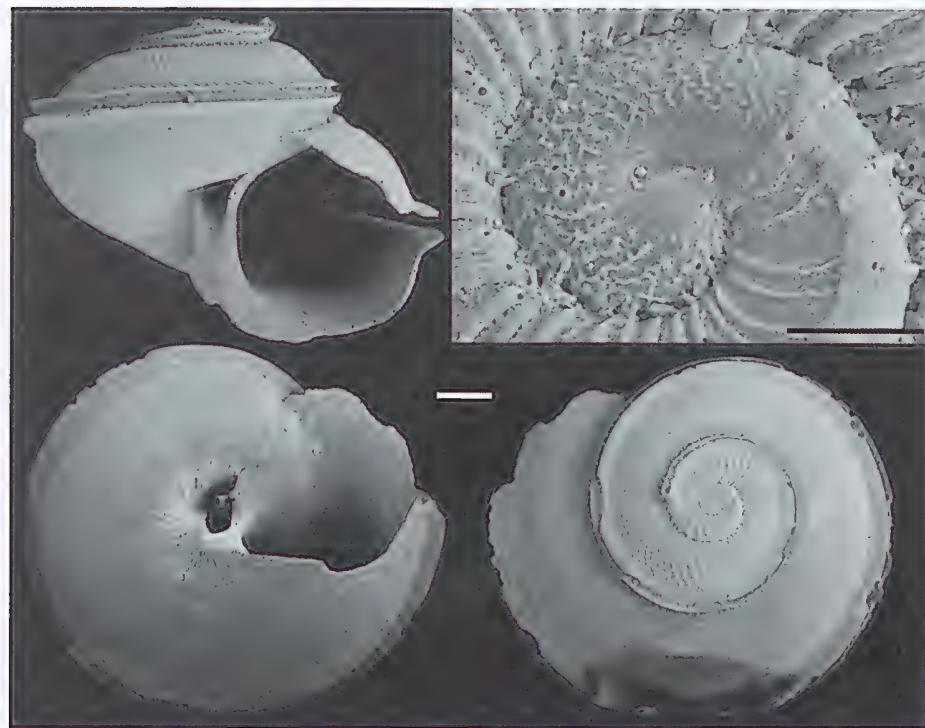


Fig. 12. *Anatomia rainesi* n. sp., paratype LACM 2910. Scale bars: shells 200 µm; protoconch 50 µm.

lamella of selenizone and suture. Shoulder with prosocline, tightly spaced, curved radials; spirals present on shoulder, absent from highest point on shoulder to suture. First spiral at beginning of selenizone; seven to nine spirals on body whorl of fully grown shell. On early whorls, spirals less than half strength of axial. Axial diminishing in strength with growth until almost absent; on later whorls, spirals stronger than faint axial. Base with undulating radials, crossed with spirals of equal strength. Interstices near selenizone rectangular with long axis in coiling direction, becoming smaller and square until disappearing towards deep, narrow umbilicus. Interstices becoming indistinct in fully grown shell; spirals predominant. Base around umbilicus only weakly sculptured by axial. Aperture dented circular; inner lip flared from lower left corner into umbilicus. Teleoconch I 2/3 of a whorl. Axial (primary) as on teleoconch II, secondary axial between primary from suture to spiral cord. Spirals of teleoconch II absent; single, strong, spiral cord in position of selenizone forming nodes at intersection with primary axial. Protoconch 3/4 whorl, 130 µm (paratype) to 150 µm (holotype), slightly sunken in. Surface smooth from suture to highest point on shoulder. Outer shoulder with irregularly jagged axial. Terminates with strong, external varix near sinusoid aperture. Varix not anchored on embryonic shell. Animal unknown.

Distribution

Easter Island.

Differential diagnoses

Anatoma s.l. *concinna* (A. Adams, 1862) from Japan lacks lamellae along the selenizone, is more globular in overall appearance and has a much wider umbilicus, based on comparisons with the illustrations provided in Habe (1951) and Thiele (1912). *Anatoma* *crispata* (Fleming, 1928) from the north-eastern Atlantic has a higher overall shape, usually lacks the lamellae along the selenizone, lacks the thickened inner lip of the aperture, teleoconch I lacks secondary radials and protoconch sculpture consists of irregular patterns. *Anatoma* s.l. *epicharis* (McLean, 1970) from Galapagos shows spiral sculpture on the shoulder from the selenizone to the suture. *Anatoma* s.l. *exquisita* (Schepman, 1908) from the Zulu Sea has more spiral threads (15 v. seven to nine) on the shoulder, based on the discussion of Thiele (1912). *Anatoma* *japonica* (A. Adams, 1862) from Japan retains the strength of the sculpture on the shoulder throughout its ontogeny or it becomes even stronger with increasing shell size. There are more spirals on the shoulder and they occupy the entire shoulder from the selenizone to the suture. *Anatoma* *lyra* (Berry, 1947) from Central California lacks secondary axials and the spiral cord on teleoconch I and the protoconch is elevated above all subsequent whorls. *Anatoma* *proxima* (Dall, 1927) from south-eastern USA has the protoconch elevated above all subsequent whorls, irregularly granulated protoconch sculpture and lacks the strong spiral in the position of the selenizone on teleoconch I. *Anatoma* s.l. *soyae* (Habe, 1951) from Japan and Alaska has the protoconch elevated above all subsequent whorls and lacks lamellae along the selenizone. *Anatoma* *yaroni* Herbert, 1986 from South Africa has the protoconch elevated above all subsequent whorls, the body whorl has 10–15 spirals and the lamellae along the selenizone are weaker.

Etymology

The species honours the collector and long-time student of the malacofauna of Easter Island, Bret Raines, of Victorville, CA, USA. He collected, and kindly made available, the material described here.

Genus *Thielella* Bandel, 1998

Thielella Bandel, 1998: 35. Type species: *Scissurella amoena* Thiele, 1912 (OD).
Pagodella Bandel, 1998: 2 (*nomen nudum*).

Description

Identical to *Anatoma*, but with protoconch of reticulate sculpture.

Differential diagnosis

Thielella has a protoconch with a honeycomb pattern, whereas *Anatoma* is either smooth or with flocculent ornamentation. It is virtually impossible to distinguish these two genera using a light microscope.

Remarks

Bandel (1998: 2) mentioned both in the German as well as the English abstract '*Pagodella*, n. gen.' among *Anatoma* and *Hainella* as species with large shells known from the

Oligocene onwards. The abstract does not contain an indication as to the type species of *Pagodella* and the genus cannot be found elsewhere in Bandel (1998); hence, *Pagodella* is a *nomen nudum*. It seems that *Pagodella* was an earlier manuscript name that was later exchanged for *Thielella*. *Thielella* is not found in the main portion of the abstract, unlike all other generic names discussed. Conversely, in the listing of new species, *Pagodella* does not appear, but *Thielella* is used.

Subfamily LAROCHEINAE Finlay, 1927

Type genus: *Larochea* Finlay, 1927 (M).

Other genera: *Larocheopsis* Marshall, 1993; *Trogoconcha* Kase & Kano, 2002.

Description

Shell trochiform to patelliform due to increased expansion rate of whorl. No slit, foramen, selenizone. Anomphalous or umbilicate with profile of base and umbilicus describing continuous curve. Protoconch smooth or with flocculate sculpture, no apertural varix, aperture simple convex curve. Operculum reduced or missing. Radula n-5-R, first through fourth laterals similar, fifth lateral enlarged or of similar size compared with other laterals, cusp similar to other laterals.

Differential diagnosis

All other subfamilies have a slit, foramen or selenizone, which is missing in all Larocheinae. The only exception is the scissurelline *Coronadoa*, which can be distinguished by its protoconch with axial sculpture and the typical scissurelline radula, with the much reduced fourth lateral and a broadened fifth lateral.

Genus *Larochea* Finlay 1927

Larochea Finlay 1927: 486. Type species: *Larochea miranda* Finlay, 1927 (M).

Genus *Larocheopsis* Marshall, 1993

Larocheopsis Marshall, 1993: 291. Type species: *Larocheopsis amplexa* Marshall, 1993 (OD).

For an excellent account of *Larochea* and *Larocheopsis*, see Marshall (1993).

Genus *Trogoconcha* Kase & Kano, 2002

Trogoconcha Kase & Kano, 2002: 26. Type species: *Trogoconcha ohashii* Kase & Kano, 2002 (OD).

Description

Shell naticiform, globular, thin, fragile, with or without umbilicus. Selenizone, slit or foramen absent. Teleoconch sculpture with axial, often with spiral sculpture. Aperture round to obliquely oval. Protoconch smooth or covered in flocculent sculpture, no apertural varix, apertural margin curved. Radula rhipidoglossate, central tooth broadest, laterals approximately equal in size and shape. Operculum rudimentary, diameter 1/4 of aperture. Animal with papillate cephalic tentacles, non-papillate epipodial tentacles, without brood pouch. Gonochoristic, no sexual dimorphism.

Differential diagnosis

Larochea has a brood pouch not found in *Trogoconcha*. *Larocheopsis* differs in the teleoconch sculpture consisting of fine pits, as opposed to distinct axials and spirals of *Trogoconcha*. *Larochea* and *Larocheopsis* lack the opeculum, which is present, but reduced, in *Trogoconcha*.

Remarks

Kase and Kano (2002) referred the specimen illustrated by Bandel (1998: pl. 23, figs 4–5, repository unknown) as ‘*La. miranda*’ to *Tr. ohashii* Kase & Kano, 2002. However, Bandel’s specimen represents *Tr. tesselata* Kase & Kano, 2002, not *Tr. ohashii* (cf. Marshall 2002). *Trogoconcha ohashii* is characterised by pustules at the intersection of the axials and the spirals, which are not evident in Bandel’s illustration. *Trogoconcha ohashii* seems also to be wider than Bandel’s specimen. Bandel’s specimen shares with *Tr. tesselata* that the axials are stronger than the spirals, whereas in *Tr. ohashii* axials and spirals are of equal strength.

Trogoconcha tesselata has only been known from two lots from the type locality at Okinawa. The species is also represented by a specimen in AMS (AMS C.377895, 21.7°S, 152.433°E, 3 km NE of west side Bylund Gillett Cay, Qld, Australia, 64–73 m: AMS SEM stub 4391).

Trogoconcha christinae n. sp.

(Fig. 13)

Material examined

Holotype and paratype. Holotype WAM S10886 and 2 paratypes AMS C.402713.

Type locality. Off Albany, WA, Australia (35.333°S, 118.333°E), 112 m, in sand and shells, 12 Mar. 1980.

Description

Shell small (holotype 0.67 mm; paratype 0.59 mm), as wide as high (width/height ratio = 1.03 (holotype), 0.96 (paratype)). Colour off-white. Teleoconch with 1.25 whorls, shoulder rounded. Sculpture of only axials, approximately 75 on body whorl. Anomphalous. Aperture obliquely oval. Selenizone, slit or foramen absent. Protoconch 133–141 µm (mean \pm SD = 137 ± 32 µm), 1.125 whorls, covered entirely with finely flocculent sculpture, apertural varix absent, apertural margin curved. Animal unknown.

Distribution

Only known from type lot.

Differential diagnosis

Trogoconcha christinae lacks the spiral sculpture of *Tr. ohashii*, *Tr. tesselata* and the fossil *Tr. marshalli* (Lozouet, 1998), is taller than these two species and lacks the umbilicus of *Tr. ohashii*.

Etymology

Named for Christine Thacker of Pasadena, CA, USA, for continuing collaboration and advice in the field as well as the laboratory.

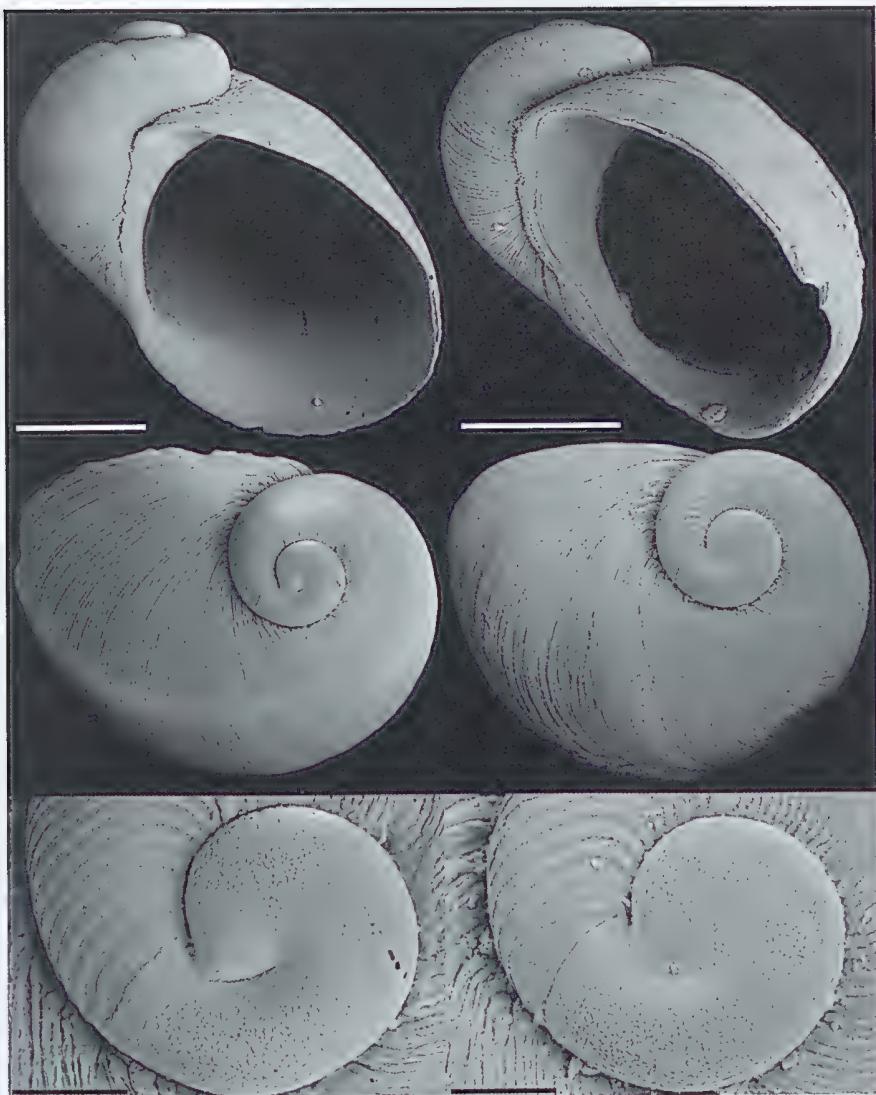


Fig. 13. *Trogloconcha christinae* n. sp. Left column, holotype WAM S10886. Right column, paratype: AMS C.402713. Scale bars: shells 200 µm; protoconch and radula 50 µm.

Subfamily SUTILIZONINAE McLean, 1989

Type genus: *Sutilizona* McLean, 1989.

Sutilizona McLean, 1989: 14–15. Type species: *Sutilizona theca* McLean, 1989 (OD).

For recent accounts on the species in the Sutilizoninae and the single genus, see McLean (1989), Haszprunar (1989) and Warén and Bouchet (2001). Warén and Bouchet (2001) elevated the subfamily to family rank.

Subfamily TEMNOCINCLINAE McLean, 1989

Type genus: *Temnocinclus* McLean, 1989.

Temnocinclus McLean, 1989; 5–7. Type species: *Temnocinclus euripes* McLean, 1989 (OD).

Other genus: *Temnozaga* McLean, 1989.

Temnozaga McLean, 1989: 9. Type species: *Temnozaga parilis* McLean, 1989 (OD).

For recent accounts on the species in the Temnocinclinae and the two genera, see McLean (1989), Haszprunar (1989) and Warén and Bouchet (2001).

Subfamily DEPRESSIZONINAE n. subfam.

Type genus: *Depressizona* n. gen.

Description

Calyptaeiform shell, umbilicate. With foramen on shoulder. Protoconch with flocculent sculpture, no varix, aperture sinusoid. Brood pouch absent. Animal unknown.

Differential diagnosis

The calyptaeiform shell distinguishes Depresszoninae from any other scissurellid subfamily. Anatominae have a trochoid shell, an open slit and the selenizone is at the periphery of the shell. Scissurellinae usually have a trochoid shell and the limpet shape of *Incisura* is attained by strongly increased expansion rate of the shell, but maintains the height of the shell. However, in Depresszoninae n. subfam., the axis is compressed, whereas the expansion rate of the shell is comparable to that of typical Scissurellinae. In Temnocinclinae, the limpet shape is also attained by a strongly increased expansion rate of the whorl, but retaining the height of the shell. All species of Temnocinclinae are endemic to the hydrothermal vent environment. Sutilizoninae, have a stronger expansion rate than Depresszoninae and the axis is compressed obliquely, maintaining more of the height of the shell. The protoconch in Sutilizoninae is pitted, whereas Depresszoninae n. subfam. have flocculent sculpture. All sutilizone species are endemic to the hydrothermal vent environment. Larocheinae lack a slit, foramen or selenizone.

Genus *Depressizona* n. gen.

Type species: *Depressizona exorum* n. sp.

Description

As for subfamily.

Remarks

Depressizona is tentatively assigned to its own subfamily due to the unique way in which limpet shape has been obtained. Protoconch sculpture is very different from any limpet-shaped scissurellids: *Sutilizona* has a pitted protoconch and *Incisura* has strong axials. Flocculent sculpture is found in *Anatoma*, with a trochiform shell and an open slit at the periphery, and in Larocheinae, with a naticiform shell and no selenizone, slit or foramen. The combination of limpet-shaped shell with a protoconch showing flocculent sculpture cannot be placed in any of the existing scissurellid genera or subfamilies.

Etymology

The name describes the overall depressed shape of the shell (Depressi-), and noting that the foramen is closed anteriorly as in *Sinezona* (-zona); feminine.

Depressizona exorum n. sp.

(Fig. 14)

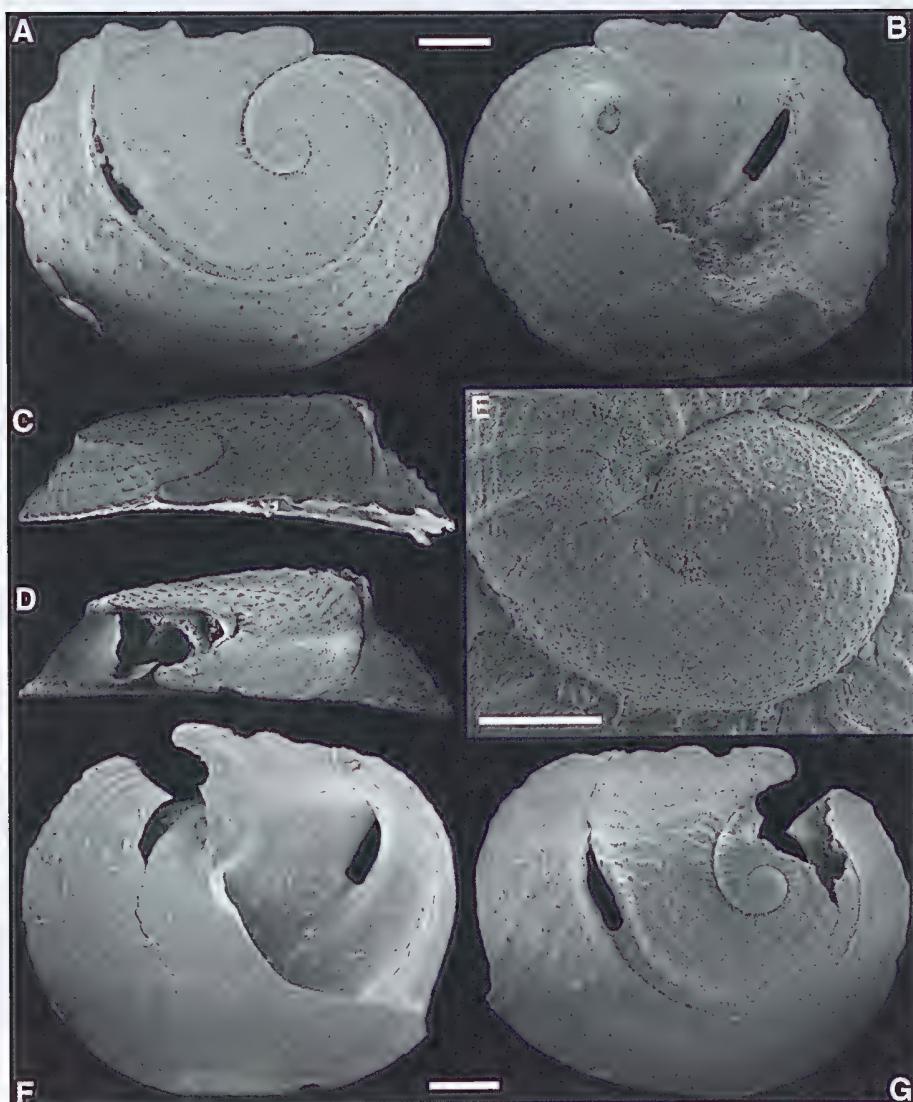
*Material examined**Holotype.* LACM 2932.*Paratype.* LACM 2933, gold coated on SEM stub.*Type locality.* Off Punta Rosalia, east of Anakena, Easter Island, 10–20 m, in sand and rubble at base of cliff, Dec. 2000. Leg. B. Raines.

Fig. 14. *Depressizona exorum* n. gen and n. sp. A–C, Holotype LACM 2932. D–G, Paratype LACM 2933. Scale bars: shells 200 µm; protoconch 50 µm.

Description

Shell calyptaeiform, thin, fragile, holotype 1.17×0.3 mm, paratype 1.24×0.35 mm. Shoulder convex, angulated at selenizone, acute angle at mid-base forming periphery of shell. Shoulder and dorsal surface of 'base' with spiral rows of pustules, sometimes connected by thin spirals, on young shell with cancellate sculpture and raised intersections of axials and spirals. Ventral surface of base with spiral sculpture of elevated elongated dots. Umbilicus forming continuous curve with base. Selenizone on shoulder, after $\frac{1}{2}$ teleoconch I whorls, selenizone of 200° , foramen teardrop-shaped closed anteriorly. Protoconch $160\ \mu\text{m}$ (paratype), $3/4$ whorls, with flocculent sculpture, no apertural varix, aperture sinusoid, keels at foramen raised forming narrow elongated chimney. Animal unknown.

Distribution

Easter Island.

Etymology

Named for Andy, G. W. Sok, Katrin, Luc and Terrie Ex of Amsterdam, The Low Countries. Genitive masculine plural of surname.

Phylogenetic analysis

Introduction

A number of characteristics have been proposed to be useful for the generic diagnoses of scissurellid genera. However, some of the supposedly diagnostic characteristics are not distributed in accordance with these proposals. For instance, '*Scissurella*' *redfernii* Rolán, 1996 has an open slit (*Scissurella*), but a protoconch with strong axial ribs (*Sinezona*). *Scissurella hoernesii* Semper, 1865 has an open slit (*Scissurella*), but a smooth protoconch (*Sukashitrochus*). The covariation of characteristics was assessed with a phylogenetic analysis of shell morphological and radular characters. Characteristics were coded according to SEM illustrations, as listed in Appendix 1. Some taxa are listed there as having SEM data available, but are not used in the present analysis for two separate reasons. First, some of the SEM illustrations did not show the feature due to orientation or quality of the specimen. Any taxon with missing data for shell morphology was excluded, because it would add unduly to the number of equally most parsimonious resolutions recovered in an analysis with more taxa than informative character states. Some exceptions were made if the species in question was of particular interest. Second, due to the limited number of characteristics, some taxa had identical character states and all but one were removed to avoid zero branch length polytomies. The data matrix is given in Appendix 2. Shell characteristics of the outgroups were coded according to Herbert and Kilburn (1986: *Emarginula*), McLean and Geiger (1998: *Emarginula*), Bayer (1965: Pleurotomariidae), Harasewych (2002: Pleurotomariidae) and Herbert (1993: Trochidae). The following characteristics were coded.

Character descriptions

Shell

The shell furnishes the majority of characteristics used for scissurellid identification and classification and is the sole data source for fossils. Thirteen characters were coded.

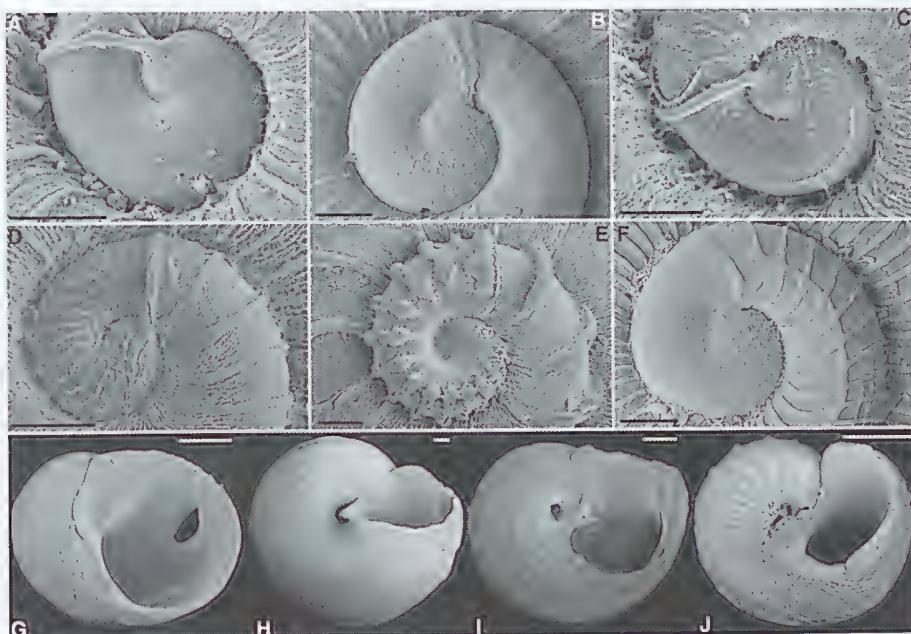


Fig. 15. Protoconch characteristics and shell character states. *A*, *Sinezona* sp. AMS C 19326/stub 4373, Masthead Island, Capricorn Group, Great Barrier Reef, Qld, Australia. *B*, *Thieleella gunteri*. AMS C.402690/stub 4356, 40 miles South of Cape Wiles, SA, Australia. *C*, *Scissurella plicata*. AMS C379418/stub 4392, Tanna Island, Hotel Tanna, Vanuatu. *D*, *Scissurella* sp. AMS C377547/stub 4370, Off Albany, WA, Australia. *E*, *Sinezona iota*. AMS C380677/stub 4378, Port Adventure, Stewart Island, New Zealand. *F*, *Anatoma australis*. AMS C400817/stub 4363, Capricorn Channel, 16.8 miles NE of North Reef, Qld, Australia. Protoconch sculpture: *A*, 0 (smooth); *B*, 1 (reticulate); *C*, 2 (spiral); *D*, 3 (irregular axial); *E*, 4 (strong axial); *F*, 6 (flocculent). Protoconch varix: *E*, 0 (absent); *B,F*, 1 (present, not connecting to embryonic cap); *A,C,D*, 2 (present, connecting with embryonic cap). Protoconch aperture shape: *A-D,F*, 0 (sinusoid); *E*, 1 (rounded). Character states of the umbilicus: *G*, closed (state 0), *Ariella subantarctica* (AMS C376612/stub 4373; Handspike Point, Macquarie Island, Australia); *H*, open without marginal carina (state 1), *Anatoma australis* (AMS C400805/ stub 4369; East of Caloundra, Qld, Australia); *I*, open, with marginal carina (state 2), *Sukashitrochus atkinsoni* (AMS C378615/stub 4376; Darwin Sandbar, NT, Australia); *J*, open, with funiculus (state 3), *Coronadoa simonsae* (LACM 66–58; Paradise Cove, Los Angeles County, CA, USA). Scale bars: shells 200 µm; protoconch 50 µm.

(1) *Protoconch sculpture*. 0: Smooth (Figs 1, 2, 15A); 1: reticulate (Fig. 15B); 2: spirals (Figs 3, 15C); 3: fine irregular axial; 4: strong axial; 5: pitted (cf. McLean 1989; Warén and Bouchet 2001); 6: flocculent (Figs 11, 12, 15F).

The sculpture of the protoconch is diverse and shows a rich complement of structural details. This fact has been recognised (Herbert 1986; Bandel 1998), although a rigorous assessment for a significant portion of species is yet to be performed. Accordingly, these sculptural details are promising for the purpose of scissurellid classification, but remain largely unexplored. Diagnostic character states cited include smooth in *Sukashitrochus*, fine axial and reticulation in *Praescissurella* Lozouet, 1998, strong axial for *Scissurella* and *Sinezona*, pitted in *Sutilizona* and reticulate in *Thieleella*.

The smooth condition of state 0 is found in Trochidae, Pleurotomariidae, four *Anatoma* species, *Larocheopsis*, *Sat. minuta*, three *Scissurella* species, *Sin. ferriezi* (Crosse, 1867), two *Trogoconcha* species and in *Temnozaga*. State 1 is diagnostic for *Thieleella*. Reticulation refers to a criss-cross pattern of fine, sharp lines of uniform thickness, as opposed to the connecting islands of unequal

thickness of state 6 (flocculent). The spirals of state 2 are delicate and can easily be eroded (e.g. *Sin. plicata* of Bandel (1998: pl. 16, fig. 2)). They are encountered in three taxa (*Sat. senni* n. sp., *Sci. coronata* Watson, 1886 and *Sin. plicata*). The irregular and undulating axialis of state 3 often show a coarse reticulate pattern on the embryonic cap, which then becomes more structured in predominantly axial elements. Often the irregular axialis are thickened on the top of the whorl, forming a spiral backbone structure; significant intraspecific variation in the development of this backbone structure can be encountered in some species. State 3 is found in two *Ariella* species, *Coronadoa*, 14 *Scissurella* species and four *Sukashitrochus* species. State 4 includes the strong axialis that do not undulate. The embryonic cap does not show the reticulations seen in species with state 3. State 4 is diagnostic for *Incisura* species and is found, in addition, in *Ar. pauperata* (Powell, 1933), six *Scissurella* species and 11 *Sinezona* species. The pitted protoconch of state 5 is diagnostic for *Sutilizona*. The flocculent sculpture of state 6 shows irregular small patches of shell material on an otherwise smooth protoconch. Sometimes they form an irregular meshwork, but the mesh is composed of elements strongly unequal in thickness, as opposed to the elements of uniform thickness of state 1 (reticulate). State 6 is found in 11 *Anatoma* species, *Depressizona* n. gen., all *Larochea* species, *Suk. pulcher* and two *Trogoconcha* species; *Tr. tesselata* Kase & Kano, 2002 was coded as state 6 because some of the protoconch shows flocculent sculpture and there is evidence of moderate abrasion. The protoconch sculpture of *Temnocinclus euripes* McLean, 1989 is unknown and coded as missing data (?); it is completely eroded (D. L. Geiger, personal observations) in the paratype illustrated in McLean (1989: fig. 4a). *Emarginula* has both flocculent sculpture, as well as spirals; hence, it was coded as polymorphic (2&6).

(2) *Protoconch varix.* 0: Absent (Figs 3, 10, 13, 14, 15D); 1: present, not connected to apex (Figs 5–9, 11, 12, 15B,F); 2: present, connected to apex and deforming area of embryonic cap (Figs 1, 2, 15A,C,D).

Close to the apertural margin of the protoconch, a subterminal varix is often found, which may form a connecting bridge to the early embryonic cap of the protoconch. This varix is absent (state 0) in Trochidae, Pleurotomariidae, seven *Anatoma* species and *Th. gunteri* (Cotton & Godfrey, 1933) among the Anatominae. Furthermore, it is missing in *C. simonsae*, *D. exorum* n. gen. and n. sp., all species of *Incisura*, *Satondella*, *Sutilizona*, *Larochea* and *Larocheopsis*, as well as in two *Ariella* species, five *Scissurella* species, two *Sinezona* species and three *Trogoconcha* species. State 1 shows this varix, but it does not connect to the embryonic cap: *Emarginula*, seven *Anatoma* species, three *Thielella* species, *Ar. halotimorpha*, eight *Scissurella* species, eight *Sinezona* species, three *Sukashitrochus* species and *Tr. marshalli* (Lozouet, 1998). State 2 shows a distinct anchoring of the varix on the embryonic cap. It is found in 12 *Scissurella* species, three *Sinezona* species and three *Sukashitrochus* species. The state is unknown and coded as missing data (?) for *Temnocinclus* and *Temnozaga*.

The connection of the varix to the embryonic cap is variable in some species (e.g. *Sin. zimmeri* n. sp.). This characteristic has not been used for generic diagnoses.

(3) *Shape of protoconch aperture.* 0: Sinusoid (Figs 1–3, 5–9, 11, 12, 14, 15A–D,F); 1: curved (Figs 10, 13, 15E).

This characteristic has not been used for generic diagnoses. The apertural margin is either sinusoid or curved. The much more common sinusoid condition (state 0) may vary from a strong curve with an amplitude of up to half the width of the whorl to a barely perceptible undulation. It is encountered in *Emarginula*, nine *Anatoma* species, three *Thielella* species, *Ar. subantarctica*, *Coronadoa*, *Depressizona* n. gen., *Sat. senni* n. sp., 21 *Scissurella* species, seven *Sinezona* species and all *Sukashitrochus* species. The less common simple convex curve (state 1) is found in Trochidae, Pleurotomariidae, five *Anatoma* species, *Th. reticulata* Bandel, 1998, two species of *Ariella*, *Incisura*, *Larochea*, *Larocheopsis* and *Trogoconcha*, as well as four species of *Scissurella*, six species of *Sinezona* and *Sut. theca* McLean, 1989. The condition is unknown for three vent species *Temnocinclus*, *Temnozaga* and *Sut. tunnicliffae* Warén and Bouchet, 2001.

(4) *Shell shape.* 0: Trochoid with elevated spire (Figs 1, 2, 5–13, 16); 1: trochoid with flat spire (Fig. 3); 2: limpet-shaped due to increased expansion rate of the whorl (Fig. 10); 3: limpet shape due to compression of shell axis (calyptraeiform; Fig. 14).

The majority of species in Scissurellidae are trochiform to naticiform with a more or less elevated spire. Most species tend to develop a more elevated spire during ontogeny; the whorls are positioned lower on the whorl with increasing size (Figs 16A,B: *Sin. cingulata* (O. G. Costa, 1861)). Thus, the application of overall shape parameters proves difficult due to rather slight differences between

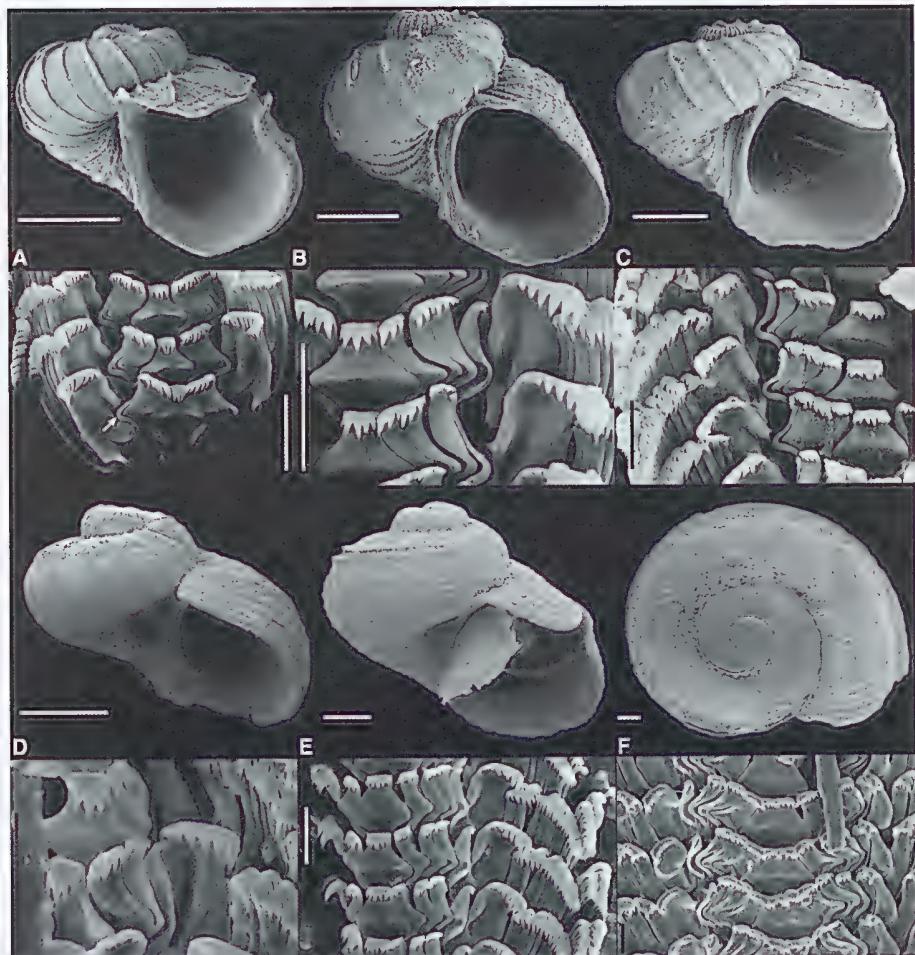


Fig. 16. Selected radulae of Scissurellidae. The shells of the specimens from which the corresponding radulae were extracted are shown. Scale bars: shells 200 µm; radulae 10 µm. *A–E*, Scissurellinae with an enlarged fifth lateral tooth. *A*, *Sinezona cingulata* (AMS C380711/stub 4370; Ceuta, Banzu, Spain). Note that the fourth lateral is hidden behind the third lateral; the arrow indicates the base of the fourth lateral. The cusp of the fourth lateral is visible on the top row on the right side. The shell is not yet fully formed: the slit is still open and the overall profile is lower. *B*, *Sinezona cingulata* (AMS C380681/stub 4378; Ceuta, Anse Sachal, Morocco). In this mature shell, the slit is closed, forming a foramen. Notice the lower position of the aperture relative to the previous whorl compared with the immature specimen to the left. *C*, *Sinezona brevis* (AMS C380172/stub 4373; East side of Island Bay, Wellington, New Zealand). The shell is not yet fully formed: the slit is still open. *D*, *Coronadoa simonsae* (LACM 66–58; Paradise Cove, Los Angeles County, CA, USA). Note the five laterals, with a much reduced fourth lateral. *E*, *Sinezona obliqua* (LACM 64–16; Iquique (near end of Ave. Baquedano), Tarapacá Province, Chile). The shell of the specimen used for radular extraction disintegrated; an alternative shell is shown. *F*, Anatominac. *Anatoma baxteri* (LACM 86–308; West of Agattu Island, Near Islands, Aleutian Islands County, AK, USA).

species and a strong ontogenetic trend to taller shell shape. Furthermore, measurement of shell parameters requires that the image is taken in a standardised fashion, a consideration that is often neglected. Hence, despite SEM imaging, shell morphometric parameters often cannot be extracted.

Shell shape is usually part of the generic diagnosis, although discrete shapes are difficult to define. Shell shape varies from trochiform (*Anatoma*) to limpet shaped (*Incisura*, *Temnocrinclus*, *Temnozaga*, *Sutilizona*, *Depressizona* n. gen.). State 0 is defined as any shell shape with moderate expansion rate of the whorl and a somewhat to distinctly elevated spire. It is most common and is diagnostic for Trochidae, *Pleurotomaria*, *Anatoma*, *Thieleella*, *Ariella*, *Coronadoa* and *Trogoconcha*. It is also found in two *Larochea* species, *Larocheopsis*, in *I. rosea*, in all but one *Scissurella* species, in all but one *Sinezona* species and in five of six *Sukashitrochus* species. State 1 includes those species in which the apex is depressed or, at most, at the same level as the top of the remainder whorls, except for the often descending terminal part of the body whorl. It is diagnostic for *Satondella* and is also encountered in *Sci. eocaenica* Bandel, 1998, *Sin. semicostata* Burnay and Rolán, 1990 and *Suk. indonesicus* Bandel, 1998.

Limpet shape is usually viewed as a derived character state and is used to diagnose those genera that feature it. Limpet shape is attained in two fundamentally different ways. State 2 is found in *Emarginula*, *Sutilizona*, *Temnocrinclus* and *Temnozaga*, as well as in three species of *Incisura*, and shows a very fast expansion rate, whereas the translation rate and, therefore, the size of the spindle remains comparable to that of the naticiform shells. The distinction between these four genera lies in the orientation of the whorl relative to the apex: in *Temnozaga*, the shell is planispiral; in *Temnocrinclus*, the apex is situated above the center of the body whorl; in *Incisura* and *Sutilizona*, the apex is in the upper one-third of the body whorl. *Depressizona* n. gen. exhibits the alternative mode of attaining limpet shape, state 3. The expansion rate of the shell is similar to that of the naticiform shells, but the translation rate is much reduced, obliterating the spindle; the profile of the shell is similar to some slipper shells (*Calyptraea*: *Calyptraeidae*).

(5) *Shape of shoulder*. 0: Rounded (Figs 1, 2, 5–13, 16); 1: angular (Figs 3, 14).

The shape of the shoulder is often indicated in generic diagnoses, although objective criteria are difficult to apply. Bandel (1998) used overall whorl shape, scalar and rounded, for generic distinctions in the *Anatoma* s.l. group, but it is difficult to apply such terms unambiguously because of extensive interspecific gradations. I distinguished two states. State 0, in which the shoulder and the base form a continuous rounded surface, intersected by the slit or foramen, is found in all *Thieleella*, *Ariella*, *Coronadoa*, *Incisura*, *Larochea*, *Larocheopsis*, *Temnocrinclus*, *Temnozaga* and *Trogoconcha* species, as well as in *Emarginula*, Trochidae, *Pleurotomaria*, eight *Anatoma* species, *Sat. minuta*, 18 *Scissurella* species, 12 *Sinezona* species, five *Sukashitrochus* species and *Sut. tunnicliffae*. State 1, in which there is a marked angle between the shoulder and the top part of the base at the intersection with the slit or foramen, is found in the minority of taxa. Eight *Anatoma* species, *Depressizona* n. gen., *Sat. senni* n. sp., seven *Scissurella* species, *Sin. beddomei*, *Suk. indonesicus* and *Sut. theca* show state 1.

(6) *Umbilicus*. 0: Absent (Figs 13, 15G); 1: present without marginal carina (Figs 11, 12, 14, 15H); 2: present with marginal carina (Figs 1–3, 5–9).

The presence or absence of an umbilicus is correlated with overall shell shape. The umbilical sculpture and associated modification of the internal lip of the aperture has been used for species diagnoses, particularly the presence of a keel. The functional significance of those keels is currently unknown.

State 0 indicates the absence of an umbilicus, where the whorls are touching one another along the axis. It is found in *Emarginula*, *Larochea*, *Larocheopsis*, *Temnocrinclus* and *Temnozaga*, as well as in two *Ariella* species, two *Scissurella* species, four *Sinezona* species, *Sut. theca* and three *Trogoconcha* species. State 1 describes the presence of an umbilicus, but the curvature of the base is continuous with the umbilical wall. This condition is diagnostic for *Anatoma*, *Thieleella* and *Depressizona* n. gen., and is also encountered in Trochidae, *Pleurotomaria*, six *Scissurella* species, eight *Sinezona* species, *Sut. tunnicliffae* and *Tr. ohashii* Kase & Kano, 2002. State 2 is characterised by a marked break between the base and the umbilical cavity, which is often adorned with a coarsely sculptured cord. It is found in *I. fossilis* (Laws, 1940), both *Satondella* species, 11 *Scissurella* species, *Sin. beddomei* and *Sukashitrochus*. The state is unknown for *Ar. pauperata* and is coded as missing datum (?).

(7) *Funiculus*. 0: Absent (Figs 1–3, 5–9, 11, 12, 14, 15H); 1: present (Figs 10, 15J; A–R, 6–9: inapplicable (Figs 13, 15G).

The funiculus is a spiral cord in the umbilical wall and has been used as a diagnostic characteristic for the generic diagnosis of *Praescissurella* Lozouet, 1998.

State 1 shows a spiral cord or funiculus that merges with the inner lower corner of the aperture. This uncommon condition is shown by *Coronadoa*, three *Incisura* species and four *Scissurella* species. For species in which there is no umbilicus, the character state is inapplicable. MacClade

(Maddison and Maddison 2000) does not allow certain letter character states, which is why additional numerical autapomorphic character states were used. The state is unknown for *Ar. pauperata* and is coded as missing datum (?).

(8) *Umbilical brood pouch.* 0: Absent (Figs 1–3, 5–15); 1: present (cf. Marshall 1993).

Umbilical modifications are known to be involved in brooding by females in *Larochea* and in *Liotiidae* (Marshall 1993; J. McLean, personal communication) and sexual dimorphism has been documented in scissurellids in *Larochea* and *Larocheopsis* (Marshall 1993), as well as *I. 'auriform'* (Hickman 1999: as *Sinezona* sp.). Gender-specific shell morphologies or their absence have otherwise not been mentioned in the literature, with the notable exception of Kase and Kano (2002) in their discussion of *Troglonconcha*; hence, these potential factors should be kept in mind, because one species may have different morphs that could be identified as two different species.

State 0 is the most common state shown in all species except those in the genus *Larochea*, which exhibit state 1.

(9) *Shell sculpture.* 0: Smooth (Fig. 10); 1: axial only (Fig. 13); 2: axial predominate over spirals (Figs 1–3, 5–9, 11, 12, 16); 3: axial equal spirals, reticulate; 4: spirals predominate over axials (Fig. 14).

Numerous sculptural elements can be distinguished. Most species have axial as well as spiral cords, producing a reticulate pattern. In addition, ribs and folds can be encountered, among other modifications. Smooth shells are rare, but those species have been assigned to particular genera (*Incisura*, *Scissurona*). Numeric differences in spiral and axial elements (e.g. *An. agulhasensis* (Thiele, 1925), *An. jacksoni* (Melvill, 1904); Herbert 1986) and differences in sculptural elements on the shoulder and the base of the shell have been used to distinguish species, but have not been applied in generic classification of scissurellids. In some species, the apertural region of the body whorl may show slightly different sculpture than the major portion of the body whorl (e.g. Fig. 11). The character state was coded according to that found on the majority of body whorls.

The teleoconch of most genera has two distinct growth phases: teleoconch I starts at the protoconch and extends to the start of the selenizone; teleoconch II comprises the shell from the start of the selenizone to the aperture of the mature shell. The sculpture on teleoconch I in the region of the selenizone can contain unique elements not seen on teleoconch II. Smooth shells (state 0) are encountered in Trochidae, two of three *Incisura* species and *Ar. subantarctica*. State 1, in which only axial elements are found to the exclusion of spirals, is uncommon. Only *An. pulchella* (Bandel, 1998), *Ar. pauperata*, *Coronadoa*, two *Scissurella* species, *Sin. iota* (Finlay, 1926) and *Tr. christinae* n. sp. show this condition. State 2, with axial predominating over spirals, is the most common condition and is found in eight *Anatoma* species, three *Thielella* species, *Ar. haliotimorpha*, both *Satondella* species, 17 *Scissurella*, 11 *Sinezona* species, four *Sukashitrochus* species and *Sut. theca*. State 3 indicates that the axial and the spirals are of equal strength. It is found in *Emarginula*, five *Anatoma* species, *Th. flemingi* Marshall, 2002, *I. fossilis*, *La. scitula* Marshall, 1993, five *Scissurella* species, *Sin. levigata*, *Sut. tunnicliffae*, *Temnocinclus*, *Temnozaga* and three *Troglonconcha* species. State 4 indicates predominate spirals over axials, found in *Pleurotomaria*, *Depressizona* n. gen., two *Larochea* species, *Larocheopsis* and *Suk. atkinsoni* (Tenison Woods, 1876).

(10) *Spiral keels on shell.* 0: Absent (Figs 1–3, 5–14, 15G,H,J, 16); 1: present (Fig. 15f).

Keels on the base of the teleoconch have been used to diagnose *Sukashitrochus*, which has also been diagnosed by a smooth protoconch. The covariation of these two character states needs to be evaluated.

State 0, without spiral keels on the base, is far more common and found in all outgroups. The presence of spiral keels (state 1) is restricted to all *Sukashitrochus* species. All other genera and species show state 0.

(11) *Slit.* 0: Open (Figs 1, 2, 11, 12, 16B); 1: closed anteriorly forming foramen (Figs 3, 5–9, 14, 15E,G); 2: absent (Figs 13, 16D).

The configuration of the slit has been considered very important in scissurellid classification and shows a remarkable degree of variation. It ranges from an open slit in which the margins of the slit remain parallel (*Anatoma*, *Scissurella*), to an open slit in which the margins converge towards the aperture (*Scissurella*), to an elongated slit in which the anterior margins are fused, forming a hole (*Depressizona* n. gen., *Sinezona*, *Sukashitrochus*, *Temnocinclus*, *Temnozaga*), to a round hole without a selenizone (*Ariella*) and, finally, to the complete absence of any trace of a slit or hole (*Coronadoa*, *Larochea*, *Larocheopsis*, *Troglonconcha*). The last condition is conventionally taken as the diagnostic characteristic for Larocheinae within Scissurellidae. The monophyly of Larocheinae remains to be demonstrated on other grounds than this single diagnostic characteristic. Currently, no other covarying

characteristics supporting Larocheinae are known. For instance, sexual dimorphism is strong in *Larocheopsis*, but undetectable in *Trogoconcha*, although this condition may be an apomorphic state within Larocheinae. The significance of the differences exemplified by *Scissurella* and *Sinezona* remains to be evaluated, particularly given the fact that, ontogenetically, the *Sinezona* stage is always preceded by a *Scissurella* stage. Herbert (1986) reached a similar conclusion with respect to this problem.

The open slit of state 0 is diagnostic for *Emarginula*, *Pleurotomaria*, *Anatoma*, *Thielella* and *Scissurella* and is also found in three *Incisura* species and *Sut. tunnicliffae*. The closed hole of state 1 is characteristic for *Ariella*, *Depressizona* n. gen., *Satondella*, *Sinezona*, *Sukashitrochus*, *Temnocinclus* and *Temnozaga* and is also found in *I. 'auriform'* and *Sut. theca*. The absence of any slit or hole (state 2) is characteristic for Trochidae, *Coronadoa*, *Larochea*, *Larocheopsis* and *Trogoconcha*.

(12) *Start of selenizone.* 0: Starts after less than 0.75 whorls (Figs 5–9, 11, 12, 14); 1: starts after more than 0.75 whorls (Figs 3, 10); 2: absent (Fig. 13).

The start of the selenizone defines the beginning of teleoconch II after variable extent of teleoconch I. Often, a distinction between a small teleoconch I of 0.5 whorls and a large teleoconch I of a full whorl or more is made, although other cut-off points have been indicated. The distribution of this characteristic is not significantly different from either normal or rectangular distribution (Fig. 4). Accordingly, I have chosen to separate the character states at a convenient, but arbitrary, 0.75 whorls, which is sufficient to examine the usefulness of this characteristic. It should be noted that intraspecific variation of the starting point of the selenizone can be at least 1/4 whorl (*An. australis* (Hedley, 1903)) and, hence, should be taken into account when diagnosing species and genera. The characteristic was coded as polymorphic (0 and 1) if the value determined for the particular specimen was within 1/8 of a whorl from 3/4 whorls, because of the 1/4 whorl intraspecific variation that may be present.

State 0 is encountered in *Emarginula*, *Pleurotomaria*, eight *Anatoma* species, *Sin. pacifica*, *Suk. pulcher*, *Temnocinclus* and *Temnozaga*. A polymorphic condition was established for four *Anatoma* species, two *Thielella* species, *Sci. ornata* and *Sut. tunnicliffae*. State 1 is found in two species of *Anatoma*, two *Thielella* species, *Depressizona*, *Incisura*, *Satondella*, 24 *Scissurella* species, 11 *Sinezona* species, five *Sukashitrochus* species and *Sut. theca*. If the selenizone is absent, it was coded as state 2, for example in Trochidae, *Ariella*, *Coronadoa*, *Larochea*, *Larocheopsis*, *Sin. levigata* and *Trogoconcha*. The condition was difficult to evaluate for *Pleurotomaria*, because most specimens have an eroded protoconch, and was coded as missing datum (?).

(13) *Position of selenizone, slit and/or foramen.* 0: At periphery of shell (Figs 11, 12, 15A–C, 16F); 1: on shoulder (Figs 1–3, 5–10, 14); A–K: inapplicable (Figs 13, 16D).

The selenizone or slitband and slit or foramen is one of the family level characteristics, although it is absent in some genera (*Coronadoa*, *Larochea*, *Larocheopsis*, *Trogoconcha*). Populations of single species may also differ in their tendency to produce a selenizone (Marshall 2002). Its position varies slightly from peripheral to on the shoulder. This slight positional difference has been used by Bandel (1998) to distinguish between genera in the *Anatoma* s.l. group, but it is difficult to apply these characteristics unambiguously.

State 0 is defined as a slit at the periphery, in which the keels are oriented approximately at right angles to the shell axis. It is found in all species of *Emarginula*, *Pleurotomaria*, *Anatoma* and *Thielella*, as well as in *Temnocinclus* and *Temnozaga*, although the overall architecture of these two groups differs radically, the former having a trochiform shell and the latter having a limpet-shaped shell due to a greatly increased expansion rate of the shell. State 1 is found further up on the shoulder and the keels are oriented at an angle inclined towards the apex. It is characteristic for the remainder of the groups, which do have a slit or hole: *Ariella*, *Depressizona*, *Incisura*, *Satondella*, *Scissurella*, *Sinezona* and *Sutilizona*. For remainder of the species that do not have a selenizone (Trochidae, *Coronadoa*, *Larochea*, *Larocheopsis*, *Trogoconcha*), this characteristic is inapplicable and is coded as an autapomorphy in each taxon: states A–K.

(14) *Keel of selenizone, slit or foramen.* 0: Moderate (Figs 1, 2, 5–9, 11, 12, 16A–C); 1: elevated anteriorly forming a chimney (Figs 3, 14); 2: low (Figs 10, 16F); A–K: inapplicable (Fig. 13, 16D).

The selenizone and the slit or foramen is bordered laterally by a pair of more or less developed spiral keels. The development of the keel is correlated with the degree of sculpturing of the shell; smooth shells usually have a hardly perceptible keel (*Incisura*, *Scissurona*). In species that lack a selenizone (e.g. *Ariella* spp.), the character was coded for the foramen. The axial growth marks of the selenizone may be coordinated with the axials of the whorl, but this seems rather useful at the specific level rather than the generic level. For species without a selenizone, this characteristic is inapplicable.

State 0 is exhibited by species in which the keel is at least $\frac{1}{4}$ the width of slit at its widest point to slightly over the width of the slit. It is the most common condition characteristic for *Emarginula*, *Anatoma*, *Thieleella*, two *Ariella* species, *Scissurella*, 12 *Sinezona* species, *Temnocinclus* and *Temnozaga*.

In state 1, the keel is much higher than the slit is wide and is diagnostic for *Depressizona* and *Satondella*. In some species, the keel is hardly perceptible and less than $\frac{1}{4}$ of the width of the slit or foramen. This state 2 is characteristic for *Incisura*, *Sutilizona* and *Pleurotomaria*. In *Sin. cingulata* (O.G. Costa, 1861), the height of the keel was, in some specimens, of intermediate height (state 0), whereas in others it was rather low (eroded?: state 2). The characteristic was coded as polymorphic (0 and 2).

For those species in which there is no selenizone, slit or foramen, this characteristic is inapplicable and is coded as autapomorphy for each taxon (states A–K), for example in Trochidae, *Coronadoa*, *Larochea*, *Larocheopsis* and *Trogoconcha*.

Radula

Relatively little is known about the radula of scissurellids, despite its recognised importance for gastropod classification in general. The radula is known for only a few selected species, which may be explained by the difficult handling of the small structures. Sasaki (1998) summarised differences in radular structure among the subfamilies: Larocheinae, Scissurellinae, Anatominiae (n-5-R); Temnocinclinae (n-3-R); Sutilizoninae (n-2-(4?)-R). The last two hydrothermal vent subfamilies share a poor distinction of lateral and marginal teeth. In Temnocinclinae, the laterals have a strong bend in the shaft near the cusp, whereas in Sutilizoninae no such distinction can be made (McLean 1989; Warén and Bouchet 2001). For this reason, the number of laterals in Sutilizoninae is difficult to assess; Sasaki (1998) quoted a range of two to four laterals. Nevertheless, the radulae of the vent families are clearly more similar to one another than either is to the remainder of scissurellid subfamilies with five laterals and an enlarged fifth (not fourth as in McLean 1989: 5; Numanami and Okutani 1980; Sasaki 1998; Geiger 2002a, unpublished data). Ponder (1998) also cited an enlarged fourth lateral as characteristic for Vetigastropoda, although most Vetigastropoda have five laterals, with the fifth enlarged. *Coronadoa simonsae* Bartsch, 1946 is unique in that a radula formula of n-4-R had been reported based on light microscopy, with an enlarged fourth lateral (Bartsch 1946). This indication was erroneous, as revealed by SEM investigation. *Coronadoa simonsae* shows a typical scissurelline radula with a triangular rachidian, similar first through third laterals, a reduced fourth lateral with pointed tip and a broadened and asymmetrically serrated fifth lateral (Fig. 16D).

Some differences in the shape of the rachidian have been noted between exemplar taxa of *Anatoma* and *Scissurella*, yet whether these observed differences apply to even a majority of the taxa included in these generic concepts remains to be demonstrated. Anatominiae have the denticles of the rachidian arranged in line parallel to the tooth rows (Fig. 16F), whereas Scissurellinae have the denticles arranged on a pointed V (Fig. 16A–E). Species of Anatominiae show a fifth lateral with a long pointed cusp that is more or less symmetrically serrated (*An. crispata* (Fleming, 1828): Hickman 1981, 1998; *An. s.l. lamellata* (A. Adams, 1862): Numanami and Okutani 1980; *An. s.l. baxteri*, *An. crispata* (North Pacific): J. H. McLean, unpublished data; Fig. 16F; *Anatoma* s.l. sp.: Sasaki 1998), although *An. euglypta* and *An. yaroni* Herbert, 1986 have a much shorter cusp than the other two species investigated (Numanami and Okutani 1980; Herbert 1986). Most Scissurellinae show a very broad fifth lateral that is asymmetrically serrated, for example *Scissurella* (*Sci. alexandrei* Montouchet, 1972 (Montouchet 1972); *Sci. cyprina* Cotton and Godfrey, 1938 (Geiger 2002b); *Sci. coronata* Watson, 1886, *Sci. declinans*, *Sin. jucunda* Smith, 1890, *Sci. rota* (D. L. Geiger, unpublished data)), *Sinezona* (*Sin. brevis*, *Sin. cingulata*: Fig. 16A,B; *Sin. beddomei* Petterd, 1884, *Sin. ferriezi*, *Sin. iota*, *Sin. pacifica* Oliver, 1915, *Sin. plicata* (D. L. Geiger, unpublished data)), *Sukashirochus* (*Suk. lyallensis* Finlay, 1926 (Marshall 1993); *Suk. atkinsoni*, *Suk. carinatus*, *Suk. pulcher* Petterd, 1884 (D. L. Geiger, unpublished data)), *Incisura* (*I. hytteltonensis* (McLean 1989); Fig. 10; *I. 'auriform'* (D. L. Geiger, unpublished data); *I. rosea* Hedley, 1904: Fig. 10), *Coronadoa* (Fig. 16D) and *Ariella* (*Ar. subantarctica* Hedley, 1916 (D. L. Geiger, unpublished data)). Marshall (2002) noted for his *Sin. bandeli* a radula formula of n-4-R. He interpreted the fifth lateral as the first marginal tooth. However, the denticles of the fifth lateral point towards the centre of the radula, whereas the denticles of the marginals (from Marshall's second marginal onwards) are directed towards the periphery of the radula and the base of the fifth lateral is significantly enlarged compared with the marginals. Accordingly, I consider *Sin. bandeli* to have a typical scissurelline radula. Some of the ambiguity in the establishment of the boundary between laterals and marginals certainly stems from the ontogenetic changes documented by Warén (1990).

Radular data for 34 of the 87 taxa included in the present study were available (Appendix 1). Illustrations of the non-Australian species are provided here, those of Australian species will be given

elsewhere (D. L. Geiger and P. Jansen, unpublished data). Some species with radular data were not included here because the SEM illustrations of all shell characteristics were unavailable (*An. s.l. lamellata*, *Sci. alexandrei*, *Suk. lyallensis*). The character states for the outgroup taxa were obtained from Hickman and McLean (1990: Trochidae), Herbert and Kilburn (1986: *Emarginula*) and Hickman (1981: *Pleurotomaria*).

- (1) *Cusp of rachidian.* 0: Denticles arranged in row parallel with row of teeth (Fig. 16F); 1: denticles arranged in V-shaped formation (Figs 10, 16A–E); 2: cusp smooth (Herbert and Kilburn 1986); 3: spoon shaped (e.g. Hickman 1981).

In state 0, The cusps of the rachidian can form a row of denticles, in which the denticles are in a row parallel with the row of teeth. This condition is found in all three *Anatoma* species, *Larochea* and *Larocheopsis*, *Temnocinclus*, *Temnozaga* and *Tr. ohashii*, but is also found in *Sci. coronata* and the three *Sukashitrochus* species. In state 1, the denticles are found on a pointed cusp, giving the cusp a V-shaped look. State 1 is in the remaining four *Scissurella* species, all seven *Sinezona* species, *Sutilizona* and is found in the only *Ariella* species for which data are available. The smooth cusp (state 2) is found in *Emarginula* and Trochidae, whereas the rachidian is spoon shaped in *Pleurotomaria* (state 3).

- (2) *Comparison of central denticle to lateral denticles on rachidian.* 0: All denticles on rachidian more or less of equal size (Figs 10, 16A–E); 1: central denticle much larger than the others (Fig. 16F); A–C: inapplicable.

State 0 is encountered in *Ar. subantarctica* as the sole representative with radular data for this genus, *Coronadoa*, *Incisura*, *La. miranda*, *Larocheopsis*, all five *Scissurella* species, all seven *Sinezona* species, two of the three *Sukashitrochus* species and *Temnocinclus*. In all three *Anatoma* species, *La. secunda*, *Suk. atkinsoni*, *Sutilizona* and *Temnozaga*, the central denticle is much enlarged compared with the others (state 1). The Rachidians of *Emarginula*, Trochidae and *Pleurotomaria* are not serrated; hence, the state is inapplicable (autapomorphic states A–C).

- (3) *Comparison of first through third laterals to fourth lateral.* 0: First through third laterals and fourth lateral similar to one another (cf. McLean 1989; Marshall 1993; Warén and Bouchet 2001; Kase and Kano 2002); 1: first through third laterals and fourth lateral dissimilar (Figs 10, 16).

The first three laterals are similar to one another in all species. However, the fourth lateral can either be similar to the first through third laterals (state 0), as shown in *Larochea*, *Larocheopsis*, *Suk. atkinsoni*, *Sutilizona*, *Temnocinclus*, *Temnozaga* and *Tr. ohashii*. The three *Anatoma* species, *Ar. subantarctica*, *Coronadoa*, *Incisura*, the five *Scissurella* species and the seven *Sinezona* species, as well as all outgroups, have a much reduced fourth lateral (Figs 10, 16), in which the cusp is only of a simple tip or a single bifurcation (state 1). The pleurotomariid radula is of a specialised rhinophiglossate type, so-called hystricoglossate (Hickman 1981, 1998). It is characterised by a much greater number of laterals, yet two discrete types can be recognised. Accordingly, the outer laterals of *Pleurotomaria* were compared with the outer laterals of the remainder of the species considered here and *Pleurotomaria* was coded 1 for character 16.

- (4) *Shape of fifth lateral.* 0: Similar to first through third laterals (cf. McLean 1989; Marshall 1993; Warén and Bouchet 2001; Kase and Kano 2002); 1: much broadened in comparison with the first through third laterals (Figs 10, 16A–E); 2: elongated in comparison with the first through third laterals (Fig. 16F; Hickman 1998).

The fifth lateral can either be similar to the first through third laterals (state 0) and is found in *Larochea*, *Sutilizona*, *Temnocinclus*, *Temnozaga* and *Tr. ohashii*. In *Sutilizona*, the distinction between laterals and marginals is very difficult, because the laterals and marginals blend smoothly into one another. Accordingly, *Sutilizona* was coded as having the fifth lateral similar to the first through third laterals (state 0), which assumes that it shares, with all other Scissurellidae, a condition with five laterals. In contrast, the fifth lateral is much broadened in *Ar. subantarctica*, *Coronadoa*, all three *Incisura* species, all five *Scissurella* species, all seven *Sinezona* species and all four *Sukashitrochus* species investigated (state 1). The coding of *Pleurotomaria* was performed as under character 16 (state 1). In the three *Anatoma* species, the fifth lateral is much elongated and essentially a hypertrophied first through third lateral (state 2).

Analysis

Exploratory phylogenetic analysis was conducted to examine the degree of covariation of the characteristics. Three main lineages in Vetigastropoda were chosen as outgroups (*Emarginula*, Trochidae and Pleurotomariidae). The fissurellid genus *Emarginula* was chosen based on the phylogenetic work of McLean and Geiger (1998) and a typical trochid

was chosen among the basal representatives as shown by Hickman (1996). Taxon labels are in accordance with the conclusions from the present analysis.

First, a more restricted data matrix of 31 ingroup and three outgroup taxa was constructed. All taxa of that matrix had radular data available. The 60% majority-rule consensus tree of 29560 equally maximum parsimonious resolutions (EMPR) with 117 steps is shown in Fig. 17 ($CI = 0.50$, $RI = 0.66$; with 26 steps of inapplicables-as-autapomorphies excluded from calculations: $CI = 0.64$).

Analysis of the full data matrix of 84 ingroup and three outgroup taxa resulted in a large number of EMPR, which exceeded the holding capacity of the computer used (Macintosh G3 500 MHz, 110 MB RAM allocated to PAUP*), because the number of terminal taxa by far exceeded the minimum length of the tree (79 steps including inapplicables-as-autapomorphies; 37 steps without them). The maximum number of EMPR that could be stored was 100 000. In order to find all minimum length islands, 10 000 replicates with numbers of trees held per replicate limited to 100 was run. The minimal-length trees were then used as a starting set for more extensive searching using branch swapping. Only trees two steps longer than the minimal tree were recovered with this strategy.

One of 30 random addition runs, lasting on average 2 days each, found the shortest trees, as shown in Fig. 18, as a 50% majority-rule consensus tree ($CI = 0.42$, $RI = 0.71$, 190 steps; with 42 inapplicables-as-autapomorphies removed: $CI = 0.25$). Any clade occurring in less than 100% of EMPRs would collapse in a strict consensus tree. Because this study is designed to investigate patterns of character state changes in a very limited character set, a majority-rule consensus tree furnishes the desired information. However, this topology should not be taken as the definitive reconstruction of scissurellid phylogenetic history.

Relationships

Some notes on the topology of the phylogenetic tree recovered are in order. Some genera recognised here are shown to be para- or polyphyletic in the phylogenetic analysis. Given the limited nature of the data matrix, no sweeping reclassification is performed here.

34 taxa

In the more restricted analysis of 34 taxa (Fig. 17), the consensus shows a fairly clear separation of Scissurellinae from the remainder of the scissurellid subfamilies. Within Scissurellinae, the three *Incisura* are grouped together, along with those species with a reduced or absent slit (*Ariella*, *Coronadoa*). *Scissurella*, *Sinezona* and *Sukashitrochus* species do not segregate in their respective genera. The *Sukashitrochus* species in the 34 taxa analysis do not form a clade, whereas the group is recovered in the 87 taxa analysis (Fig. 18), but *Sukashitrochus* is not part of Anatominae. There is a strong phylogenetic signal that groups *Larochea* with *Larocheopsis*, as well as Temnocrininae and Sutilizoninae, yet the placement of *Trogoconcha*, as well as the three *Anatoma* species, among these basal members is uncertain.

87 taxa

Figure 18 shows the consensus trees for all 87 taxa analysed. The overall pattern of Anatominae and Larocheinae plus Temnocrininae plus Sutilizoninae as sistergroups is identical to the 34 taxa analysis.

Scissurellinae includes *Ariella*, *Coronadoa*, *Depressizona* n. gen., *Incisura*, *Satondella*, *Scissurella*, *Sinezona* and *Sukashitrochus*. The traditional genera are reasonably well recovered, given the limited data set. Some stray taxa have to be noted that should not

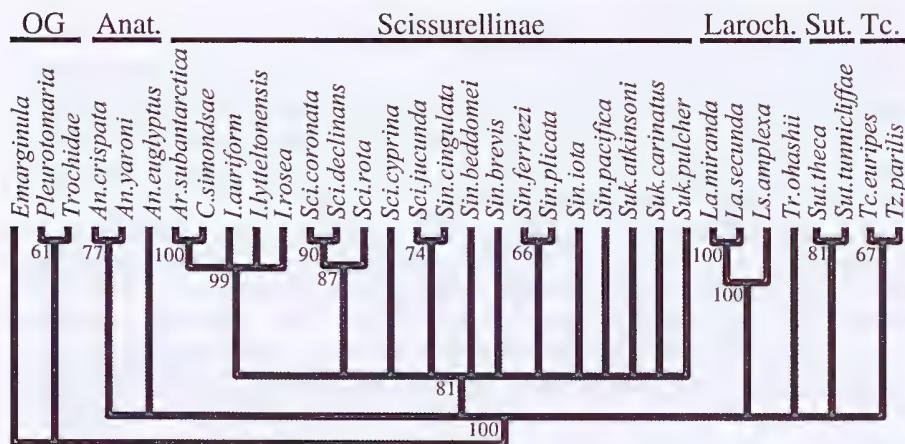


Fig. 17. A 60% majority-rule consensus tree of 29 560 equally parsimonious resolutions with 117 steps for 34 taxa with radular data available. Numbers under the nodes are percentage values >60%. Only values of 100% are retained on a strict consensus tree. OG, Outgroups; Anat, Anatominae; Laroch, Larocheinae; Sut, Sutillizoniae; Tc, Temnocinclinae. Abbreviations of generic names are as elsewhere.

distract from the overall pattern that emerges (e.g. *Sci. jucunda* in *Sinezona*). *Sukashitrochus* is a clearly supported by an analysis using shell characteristics only (tree not shown) as well as with the additional radular characters, despite the fact that only three of the six species had radular data available (Fig. 18). In contrast, the three *Sukashitrochus* species in the 34 taxa matrix are found in the broad basal polytomy. Hence, more extensive taxon sampling, despite some missing data, can provide additional phylogenetic signals. The present analysis supports findings by Kearney (2002). *Sukashitrochus* is situated within Scissurellinae and is well-separated from Anatominae.

McLean (1989) noted radular similarities between *Sukashitrochus* and *Anatoma*. The two genera share a rachidian in which the cusp forms a straight, serrated line. However, the fifth lateral is broadened in *Sukashitrochus*, which is similar to the condition in the remainder of Scissurellinae and distinct from the elongated fifth laterals in *Anatoma* (the radular condition in any *Thieleella* species is unknown). Accordingly, in the best-case scenario, the radular data are ambivalent as to the subfamilial placement of *Sukashitrochus*. The data become more clear-cut once shell data are included. The ‘diagnostic’ smooth protoconch of *Sukashitrochus* (cf. Herbert 1986), is only found in the species described by Herbert (1986: *Suk. mariasi*). The cautious notes by earlier authors (Numanami and Okutani 1990; Marshall 1993; Amitov and Zhegallo 1998; Bandel 1998; Lozouet 1998; Sasaki 1998) as to McLean’s (1989) placement of *Sukashitrochus* in Anatominae are borne out and the genus is here reassigned to Scissurellinae.

Satondella and *Depressizona* n. gen. form a small clade in Scissurellinae, based solely on shell characteristics. Radular data are not available for either of the two genera. The placement of *Depressizona* n. gen. in *Satondella* is due to the elevated keels of the selenizone and foramen. *Incisura* is also found within Scissurellinae. The two *Ariella* species are widely separated among the *Sinezona* species. This leads to further credence of Marshall’s (2002) position, arguing that the absence of the selenizone is only an extreme form among the variations of selenizone length (Fig. 4). However, there is no information beyond shell data that could clarify the situation. *Coronadoa* is found within *Sinezona*; the absence of a slit, foramen or selenizone in *Coronadoa* has quite clearly evolved in parallel to Larocheinae.

Within Anatominae, the four *Thieleella* species are in one grade at the periphery of the subfamily. Their association is based on the sole differentiating characteristic of the protoconch with reticulate sculpture. Additional data are required to clarify the position and the monophyly of *Thieleella*.

The third large clade comprises Sutilizoninae plus Temnocinclinae plus Larocheinae. The major grouping factor for all three subfamilies is the radula with poorly differentiated laterals. In particular, the fourth and fifth laterals are similar to the first through third laterals, unlike in Scissurellinae, with a reduced fourth lateral and a broadened fifth lateral, and unlike Anatominae, also with a reduced fourth lateral but an elongated fifth lateral. The position of the fossil *Tr. marshalli* may be attributed to the lack of radular data. Within Larocheinae, *Larochea* is recovered as a clade diagnosed by the brood pouch, whereas *Trogleoncha* is a basal grade.

Sutilizoninae has been elevated by Warén and Bouchet (2001) to family rank. The present analysis shows that Sutilizoninae is more closely related to Temnocinclinae and Larocheinae than to Anatominae and Scissurellinae. The main basis for the distinction of the two clades is the radula structure discussed above. Whether Sutilizoninae should be elevated to family rank can be debated, but if one chooses to do so, then Temnocinclinae and Larocheinae should be included under Sutilizonidae. The classification used here unites all scissurellids in a single family and does not formally recognise the (Sutilizoninae, Temnocinclinae, Larocheinae) clade; there is no need to name every clade.

Discussion

Easter Island Scissurellidae

The present contribution describes the first group of scissurellid species from Easter Island. The standard work of Rehder (1980) did not list any member from this family, nor were any included in the additions made by DiSalvo *et al.* (1988) or Osorio and Cantuarias (1989). Raines (2002) illustrated four of the five new species as unidentified specimens. Representatives of Scissurellidae are known from the islands closest to Easter Island, namely French Polynesia (Salvat and Rives 1975; D. L. Geiger, personal observations), Hawaii (Kay 1979) and the Galapagos Islands (McLean 1971; Finet 1993).

The four species described here can be readily distinguished from one another. First, overall shell shape separates *Anatoma rainesi* n. sp. from the other three species. The other three species are distinguished by the protoconch sculpture: smooth in *Sci. alto* n. sp., with spiral threads in *Sat. senni* n. sp. and with strong axials in *Sin. zimmeri* n. sp. The reliance on protoconch sculpture alleviates the problem associated with the problematic characteristics of open slit versus closed foramen, because the open slit is a mandatory stage in the development of a foramen in the Easter Island species. The two species with a foramen may be difficult to distinguish using a light microscope. In fully grown specimens of *Sat. senni* n. sp., the raphe anterior to the foramen is at a discrete angle to the remainder of the curve described by the selenizone and the foramen, whereas in *Sin. zimmeri* n. sp. the raphe is continuous with the curve described by the selenizone and the raphe. In addition, the arc of foramen plus selenizone is usually greater than half a whorl in *Sat. senni* n. sp., whereas in most *Sin. zimmeri* n. sp. it is less than half a whorl. Immature specimens of *Sci. alto* n. sp. and *Sin. zimmeri* n. sp. are very difficult to distinguish using a light microscope, whereas *Sat. senni* n. sp. has weaker axial sculpture than the other two species.

The overall faunal affinity of Easter Island is to the central, Indo- and western Pacific for all groups studied, including molluscs (Rehder 1980), ants (Morrison 1997), fish

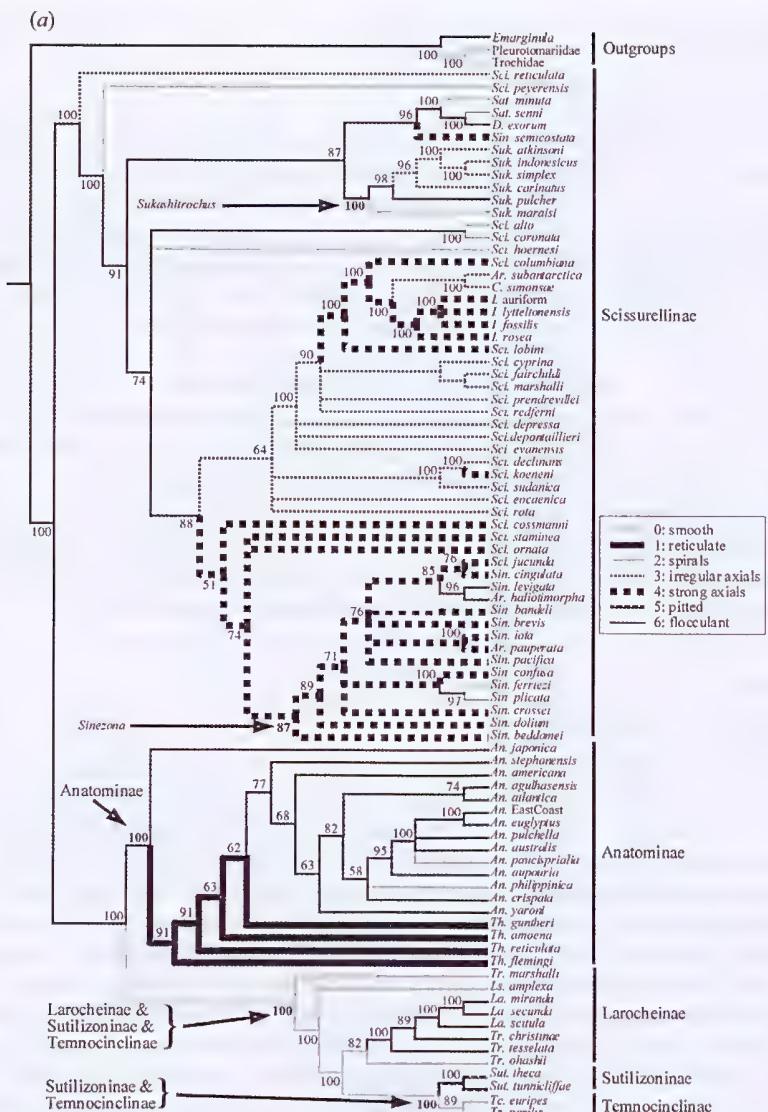


Fig. 18. A 50% majority-rule consensus tree of 100 000 equally parsimonious resolutions with 19 steps for 87 taxa (Appendix 2). Numbers under the nodes are average percentage values > 50%. Only values of 100% are retained on a strict consensus tree. (a), The character states for protoconch sculpture are mapped. The distinction of *Scissurella* and *Sinezona* is not recovered by protoconch sculpture. The ‘diagnostic’ smooth protoconch of *Sukashitrochus* (grey line) is found only in *Suk. maraisi*. (b), The character states for the configuration of the slit/foramen are mapped. The transition is always from open slit to foramen or absence; the slit is never secondarily opened again. *Scissurella* and *Sinezona* are distinguished by a slit in *Scissurella* and a foramen in *Sinezona*. *Sukashitrochus* is a derived group within *Scissurella* that has independently closed the slit to a foramen. Significant character-state transitions are mapped on the tree. Taxa in bold face have radular data available. Brood pouch, presence of a brood pouch in the columellar region (character 7); Keel, keels on base of shell (character 10); Ks, keel of selenizone (character 14); Rc, Cusp of Rachidian (character 15); L4, condition of the fourth lateral compared with the first through third laterals (character 17); L5, condition of the fifth lateral (character 18); ia, inapplicable.

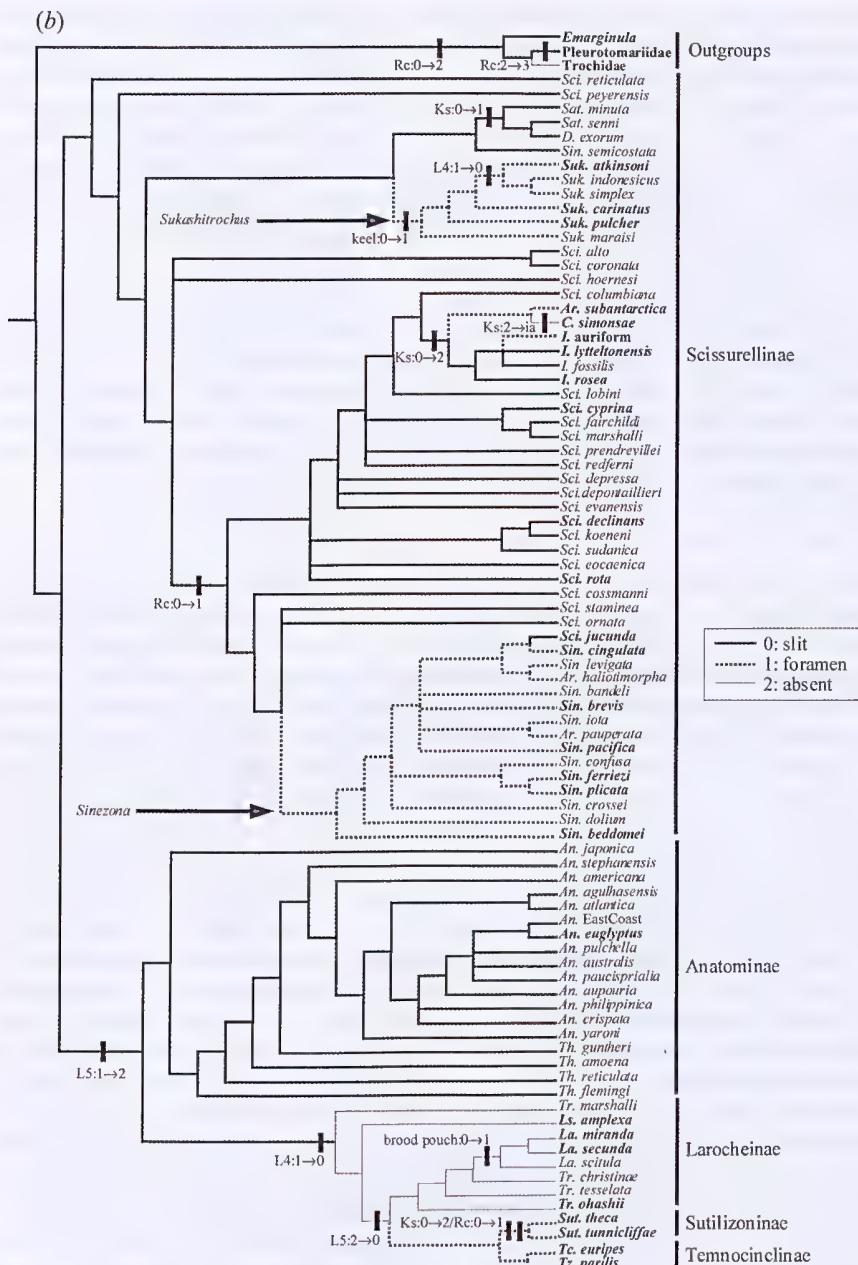


Fig. 18. (continued)

(Randall 1998) and ostracods (Whatley and Jones 1999). Rehder (1980) identified the greatest affinity to the Indo-Pacific (34.5% species shared), followed by Pitcairn, Rapa and Kermadecs (15%) and Hawaii (15%). If the areas these provinces are occupying are taken into account, then the closer islands (Pitcairn, Rapa and Kermadecs) and Hawaii show the strongest faunal affinity with Easter Island.

Satondella senni n. sp. sheds some light on the faunal affinity. All described (*Sat. minuta*) and one undescribed species of *Satondella* are from Indonesia and Australia, respectively, pointing to an eastward dispersal. The spiral sculpture on the protoconch is also shared with an Indo-Pacific species, namely *Sci. plicata*. The other scissurellid genera reported here from Easter Island have both Indo-Pacific as well as eastern Pacific representatives. The sculptural details, particularly the protoconch sculpture of *Anatoma* and *Scissurella*, do not harbour any geographic information. Accordingly, Scissurellidae of Easter Island show a weak Indo-Pacific affinity and no relationship to either eastern Pacific or Hawaii can be extracted.

The degree of endemism of Easter Island is remarkable. Rehder (1980) calculated a value of 42% for the mostly littoral species he surveyed. With the addition of the subtidal species discussed by Raines (2002), this figure has dropped now to 37%, which is still in the high range of endemicity values of 13.5%–50% of various Pacific Islands, including Hawaii (Rehder 1980). On available data, all five species and the new genus are endemic to Easter Island, but because Scissurellidae is still a poorly known family, some of the Easter Island species may have a wider range.

Shell characteristics for generic diagnosis

Bandel (1982) noted that the protoconch of ‘archaeogastropods’ is very plastic with respect to the sculpture it exhibits and concluded that protoconch sculpture is unsuitable for the higher classification of ‘archaeogastropods’, in contrast with its usefulness in caenogastropods. Vermeij (2002) also concluded that protoconch sculpture has little potential for phylogenetic analysis due to extensive interspecific variations that are ecologically mediated. Gili and Martinell (2000) and Solsona and Martinell (1999) demonstrated that protoconch morphology in closely related species of *Cyclope* (Caenogastropoda: Nassariidae) and *Natica* (Caenogastropoda: Naticidae), respectively, can change dramatically, reflecting altered larval ecology, without affecting teleoconch morphology. Nevertheless, protoconch sculpture has been cited both for diagnoses of scissurellid genera, such as *Sukashitrochus* by Herbert (1986) and *Thielella*, by Bandel (1998), as well as *Sutilizoninae* by McLean (1989). The value of the protoconch sculpture is variable, even within a single vetigastropod family, as demonstrated in the present study. *Anatoma* exhibits two of the six conditions (smooth, flocculent), *Thielella* is diagnosed by the reticulate protoconch sculpture, *Incisura* shows the strong axials that are also shared with other *Sinezona*, *Scissurella* and *Sukashitrochus* species and *Sutilizona* shows the pitted protoconch unique among Scissurellidae. However, the large group of *Scissurella*, *Sinezona* and *Sukashitrochus* show five discrete protoconch types intermixed. Among species of *Sinezona* and *Scissurella*, many have either strong axials ribs or fine irregular axials on the protoconch, respectively. However, the exceptions in species of both genera are too numerous to use protoconch sculpture as a diagnostic characteristic for genera in Scissurellinae (Fig. 18a). It is of note that the diagnostic value of protoconch sculpture is inversely correlated with the number of taxa to be diagnosed. All genera for which protoconch sculpture is diagnostic contain few species (four in *Incisura*, two in *Sutilizona* and four in *Thielella*), whereas those genera in which significant homoplasy could be demonstrated are more speciose (14 in *Anatoma*, 25 in *Scissurella*, 13 in *Sinezona* and six in *Sukashitrochus*).

The presence or absence of a subterminal varix on the protoconch is also shown to be highly variable within and between the groups. Anatominae show only a weak development of the varix (states 0 and 1), in which the varix does not form a distinct connection to the

embryonic cap. In Scissurellinae, the condition is most variable, showing all possible arrangements. The smaller groups (*Incisura*, *Sutilizona*, *Larochea*, *Satondella*), with three to four species each, all lack a varix, whereas three of four *Trogoconcha* species lack the varix.

The shape of the protoconch aperture is equally variable. Larocheinae (*Larochea*, *Larocheopsis*, *Trogoconcha*) is characterised by a rounded aperture, as is *Incisura*. Within Anatominae and Scissurellinae, the sinusoid aperture is more common. The amplitude of the sinusoid aperture shape is rather variable within species and, similar to the length of the selenizone, the rounded aperture could be viewed as a sinusoid aperture with zero amplitude. Intraspecific variability of protoconch characteristics is usually not reported and is most likely underestimated, as indicated by Rouget and Neige (2001) for ammonites.

Shell shape is, to a certain extent, diagnostic. The limpet-shaped forms (*Temnocinclus*, *Temnozaga*, *Sutilizona*, *Depressizona*) are characterised by shell shape, although the shape seems to have evolved several times. The flattened top of the spire is found in all *Satondella* species and also in *Sci. eocaenica* Bandel, 1998. The shape of the shoulder, the condition of the umbilicus (Fig. 18b) and shell sculpture are quite variable and do not seem to be useful as diagnostic characteristics of generic taxa. Wagner (2001) and Vermeij (2002) reached similar conclusions. However, the presence of a brood pouch diagnoses *Larochea*, whereas the spiral keel on the base diagnoses *Sukashitrochus*.

The condition of the slit or foramen is diagnostic (Fig. 18b), which suggests that the different conditions are due to underlying modifications of the mantle, as is the case in Fissurellidae (McLean and Geiger 1998). Wagner (2001) and Vermeji (2002) also pointed out that shell characteristics caused by modifications of the mantle usually have a strong phylogenetic signal. In particular, the foramen separates *Sinezona* and *Sukashitrochus* from *Scissurella*, which has a slit. Accordingly, the conflicting information found in protoconch sculpture and slit/foramen has been decided in favour of the latter. The absence of a slit or foramen in *Larochea*, *Larocheopsis* and *Trogoconcha* is diagnostic. The closure of the slit resulting in a foramen has taken place several times: in *Sukashitrochus*, *Sinezona*, *I. 'auriform'* and *Ar. subantarctica*. In addition, the slit and foramen have been lost twice: in *Coronadoa* and in *Trogoconcha*, *Larochea* and *Larocheopsis*. In contrast, the opening of a foramen into an open slit has only occurred in *Sci. jucunda* within *Sinezona* and in *Sutilizoninae* plus *Temnocinclinae* within Larocheinae (Fig. 18a,b). This indicates a driven trend in which the direction of character-state changes is biased, as discussed by Wagner (2001). A driven trend needs not to lead to an increase in homoplasy, because change frequency (homoplasy) and the direction of change (driven trend) are independent (*contra* Wagner 2001). Even if one argued that once the unidirectional character-state change had occurred then a reversal would be precluded, homoplasy in characteristics affected by a driven trend would decrease, not increase. The opening of the foramen to a slit in *Sci. jucunda* is due to the stray placement of this particular species.

However, the beginning of the selenizone is more difficult to interpret and its application in generic diagnoses is questionable (Fig. 4). The extensive intraspecific variability of at least $\frac{1}{4}$ whorl further impedes the application of this characteristic. However, the peripheral position of the selenizone clearly separates Anatominae from the remainder of Scissurellidae.

The radular data, although highly incomplete, did help show some patterns more clearly (Figs 17, 18b). The more basal split of Anatominae plus Scissurellinae and Larocheinae plus Sutilizoninae plus Temnocinclinae is based on the arrangement of the fourth and fifth laterals. These are dissimilar to the first through third laterals in the former, whereas they are similar in the latter. The shape of the rachidian and the shape of the fifth lateral separates

Anatominae from Scissurellinae. The radular data set has approximately 60% missing data (missing data of entire data set: 15%), yet seems to contribute significantly to the understanding of character evolution in Scissurellidae.

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Appendix 1. Summary of information available on scissurellid species-level taxa

Species	DR	LM	SEM	PC	R	EA	H	Z	References
<i>Anatoma</i>									
' <i>An. aequatorina</i> ' Hedley, 1899									
<i>An. aguilhasensis</i> (Thiele, 1925) (<i>Scissurella</i>) ¹	•	•	•	•	•	•	IO	Thiele 1925; Herbert 1986; D. L. Geiger, unpublished data.	
<i>An. alta</i> (Watson, 1886) (<i>Scissurella</i>)	•	•	•	•	•	•	SA	Watson 1886; Thiele 1912; Bandel 1998	
<i>An. americana</i> Bandel, 1998	•	•	•	•	•	•	NA	Bandel 1998	
<i>An. aupouria</i> (Powell, 1937) (<i>Schizotrochus</i>)	•	•	•	•	•	•	NZ	Powell 1937, 1979; D. L. Geiger, unpublished data	
<i>An. atlantica</i> (Bandel, 1998) (<i>Hainella</i>)	•	•	•	•	•	•	NA	Bandel 1998; D. L. Geiger, unpublished data	
<i>An. australis</i> (Hedley, 1903) (<i>Scissurella</i>)	•	•	•	•	•	•	AU	Thiele 1912; Jansen 1999; D. L. Geiger, unpublished data	
<i>An. costamagnensis</i> Marguet, 1984 [†]	•	•	•	•	•	•	EU	Bandel 1998	
<i>An. crispatia</i> (Fleming, 1828) (<i>Scissurella</i>) ²	•	•	•	•	•	•	NA	Watson 1886; McLean 1967, 1989; Bandel 1982, Hieckman 1998 (as <i>Scissurella crispatia</i>), Okutani and Hasegawa 2000; Redfern 2001	
+ <i>Sci. chiricava</i> Dall, 1919							NP	Burnay and Rolán 1990; Giannuzzi-Savelli 1994; D. L. Geiger, unpublished data	
+ <i>Sci. (Schizotrochus) kelseyi</i> Dall, 1905							NP		
+ <i>Sci. palaeomphaloides</i> Nordsieck, 1974							NP		
<i>An. danica</i> Bandel, 1998 [†]	•	•	•	•	•	•	EU	Bandel 1998	
<i>An. equatoria</i> (Hedley, 1899) (<i>Scissurella</i>)	•	•	•	•	•	•	TP	Thiele 1912	
<i>An. englyptia</i> (Pelseneer, 1903) (<i>Scissurella</i>)	•	•	•	•	•	•	AN	Thiele 1912; Numanami and Okutani 1990; Bandel 1998; Forcelli 2000	
<i>An. finlayi</i> (Powell, 1937) (<i>Schizotrochus</i>)	•	•	•	•	•	•	NZ	Powell 1937, 1979; Jansen 1999; D. L. Geiger, unpublished data	
<i>An. indonesia</i> Bandel, 1998	•	•	•	•	•	•	IP	Bandel 1998	
<i>An. jacksoni</i> (Melvill, 1904) (<i>Scissurella</i>)	•	•	•	•	•	•	IO	Yaron 1993; D. L. Geiger, unpublished data	
<i>An. japonica</i> (A. Adams, 1862) (<i>Anatomus</i>)	•	•	•	•	•	•	NP	Thiele 1912; Habe 1951; Herbert 1986; Okutani and Hasegawa 2000; Higo <i>et al.</i> 2001	
<i>An. lyra</i> Berry, 1947 (<i>Scissurella (Anatoma)</i>)	•	•	•	•	•	•	IO?	Bandel 1998	
							NP	McLean 1967, 1989; D. L. Geiger, unpublished data	

(continued next page)

Appendix 1. (continued)

Species	DR	LM	SEM	PC	R	EA	H	Z	References
<i>An. paucispinaria</i> (Bandel, 1998) (<i>Hainella</i>)	•	•							IP Bandel 1998
<i>An. philippinica</i> (Bandel, 1998) (<i>Hainella</i>)	•	•							IP Bandel 1998
<i>An. proxima</i> (Dall, 1927) (<i>Scissurella</i>)	•	•	•	•	•				NA Bandel 1998
<i>An. pulchella</i> (Bandel, 1998) (<i>Hainella</i>)	•	•	•	•	•				IP Bandel 1998
<i>An. rainesi</i> n. sp.	•	•	•	•	•				CP Raines 2002 (as <i>Anatoma</i> sp.); this study
<i>An. regia</i> (Mestayer, 1916) (<i>Scissurella</i>)	•	•	•	•	•				NZ Fleming 1948; Powell 1979; D. L. Geiger, unpublished data
<i>An. sagamiana</i> Okutani, 1964	•	•	•	•	•				NP Okutani 1964; D. L. Geiger, unpublished data
<i>An. stephanensis</i> Bandel, 1998 [†]	•	•	•	•	•				EU Bandel 1998
<i>An. turbinata</i> A. Adams, 1962 (<i>Anatomus</i>) ¹	•	•	•	•	•				NP Thiele 1912; Habe 1951; Okutani and Hasegawa 2000; Higo <i>et al.</i> 2001
	•	•	•	•	•				IP Bandel 1998; Jansen 1999 (both as <i>An. agulhasensis</i>); D. L. Geiger, unpublished data
<i>An. umbilicata</i> (Jeffreys, 1883) (<i>Scissurella</i>)	•	•	•	•	•				NA Thiele 1912; Giannuzzi-Savelli <i>et al.</i> 1994; Bandel 1998
<i>An. yaroni</i> Herbert, 1986	•	•	•	•	•				IO Herbert 1986; D. L. Geiger, unpublished data
<i>An.</i> East Coast	•	•	•	•	•				AU Jansen 1999; D. L. Geiger, unpublished data
<i>Thielella</i>									
<i>Th. amoena</i> (Thiele, 1912) (<i>Scissurella</i>)	•	•	•	•	•				AN Thiele 1912; Numanami and Okutani 1990; Bandel 1998
<i>Th. gunteri</i> (Cotton & Godfrey, 1933)	•	•	•	•	•				AU Cotton 1959; Jansen 1999; D. L. Geiger, unpublished data
(<i>Schizotrochus</i>)									
<i>Th. flemingi</i> Marshall, 2002	•	•	•	•	•				NZ Fleming 1948 (as <i>Schiz. mantelli</i> ; Marshall 2002); Powell 1979 (as <i>An. mantelli</i> ; Marshall 2002); Marshall 2002; IP Bandel 1998
<i>Th. reticulata</i> Bandel, 1998	•	•	•	•	•				
<i>Anatoma</i> or <i>Thielella</i> (protoconch sculpture unknown)									
<i>aedonita</i> Watson, 1886 (<i>Scissurella</i>)	•	•	•	•	•				IO Watson 1886; Thiele 1912
<i>aetheria</i> Melvill & Standen, 1903 (<i>Scissurella</i>)	•	•	•	•	•				IO Melvill and Standen 1903; Thiele 1912
<i>africana</i> Barnard, 1963 (<i>Scissurella</i>)	•	•	•	•	•				IO Barnard 1963 ³
<i>baxteri</i> McLean, 1984 (<i>Anatomus</i>)	•	•	•	•	•				NP McLean 1984, unpublished data; D. L. Geiger, unpublished data
<i>conica</i> D'Orbigny, 1841 (<i>Scissurella</i>)	•	•	•	•	•				SA Forcelli 2000
<i>concinna</i> A. Adams (<i>Anatomus</i>)	•	•	•	•	•				NP Thiele 1912; Habe 1951
<i>disiformis</i> Golikov & Sirenko, 1980	•	•	•	•	•				NP Golikov and Sirenko 1980
(<i>Scissurella</i> (<i>Schizotrochus</i>))	•	•	•	•	•				

TP	McLean 1971; Finet 1993
IP	Thiele 1912
NP	McLean 1971
NP	Thiele 1912; Habe 1951; McLean 1967; Kuroda <i>et al.</i> 1971;
	Kay 1979; Numanami and Okutani 1990; Okutani and Hasegawa 2000; Higo <i>et al.</i> 2001
NZ	Thiele 1912 (<i>nomen dubium</i> ; Marshall 2002)
IP	Thiele 1912; Okutani and Hasegawa 2000
NP	Golikov and Gublin 1978
AN	Numanami and Okutani 1990
NP	Habe 1951; McLean 1967; Higo <i>et al.</i> 2001
IO	Barnard 1964
EU	Lozouet 1986, 1998; Bandel 1998
NA	Watson 1886; Thiele 1912
NZ	Marshall 1993
SP	Hedley 1916; D. L. Geiger, unpublished data
NP	Bartsch 1946; this study
CP	This study
AU	Jansen 1999; Hickman 1999; D. L. Geiger, unpublished data
NZ	Bandel 1998
NZ	Pelseneer 1899; Bourne 1910; McLean 1989; Bandel 1998;
	this study
NZ	Thiele 1912; Powell 1979; Bandel 1998; D. L. Geiger,
	unpublished data
AU	Jansen 1999; this study
SA	Watson 1886; Thiele 1912
AU	Cotton 1959
NZ	Marshall 1993

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Appendix 1. (continued)

Species	DR	LM	SEM	PC	R	EA	H	Z	References
<i>La. scitula</i> Marshall, 1993	•	•							NZ Marshall 1993
<i>La. secunda</i> Powell, 1937	•	•	•						NZ Marshall 1993
<i>Larocheopsis</i>									
<i>Ls. amplexa</i> Marshall, 1993	•	•	•						NZ Marshall 1993
<i>Satondella</i>									
<i>Sat. minuta</i> Bandel, 1998	•	•	•						IP Bandel 1998
<i>Sat. senni</i> n. sp.	•	•	•						CP Raines 2002 (as <i>Satondella</i> sp.); this study
<i>Sat. tabulata</i> (Watson, 1886) (<i>Schismopoe</i>)	•	•	•						NA Watson 1886; Thiele 1912; Redfern 2001 (?)
<i>Scissurella</i>									
<i>Sci. alexandrei</i> Montouchet, 1972	•	•	•						SA Montouchet 1972
<i>Sci. alto</i> n. sp.	•	•	•						CP Raines 2002 (as <i>Scissurella</i> sp.); this study
<i>Sci. aspera</i> Philippi, 1844	•	•	•						NA Nordsieck 1968
<i>Sci. bertheloti</i> d'Orbigny, 1839	•	•	•						NA Nordsieck 1968
<i>Sci. bonyensis</i> Powell, 1933	•	•	•						NA Powell 1933
<i>Sci. cebiana</i> (Bandel, 1998) (<i>Anatoma</i>)	•	•	•						IP Bandel 1998
<i>Sci. / An.? clathrata</i> Strebler, 1908 (<i>Scissurella</i>)	•	•	•						AN Thiele 1912; Forcelli 2000
<i>Sci. columbiana</i> (Bandel, 1998) (<i>Schismopoe</i>)	•	•	•						SA Bandel 1998
<i>Sci. coronata</i> Watson, 1886	•	•	•	•	•	•	•		IP Watson 1886; Thiele 1912; Jansen 1999; D. L. Geiger, unpublished data
<i>Sci. costata</i> d'Orbigny, 1824	•	•	•	•	•	•	•		NA Vaysiere 1894; Pelseneer 1899; Nordsieck 1968; Bandel 1982, 1998; Poppe and Goto 1991; Giannuzzi-Savelli et al. 1994
<i>Sci. cyprina</i> Cotton and Godfrey, 1938	•	•	•	•	•	•	•	AU Cotton 1959; Jansen 1999; Geiger 2002b	
<i>Sci. dalli</i> Bartsch, 1903	•	•	•	•	•	•	•	SA	
<i>Sci. declinans</i> Watson, 1886	•	•	•	•	•	•	•	IP Thiele 1912; Watson 1886; Jansen 1999; D. L. Geiger, unpublished data. Not Bandel (1998) (= <i>Suk. atkinsoni</i>)	
<i>Sci. depontaillieri</i> Cossman, 1879	•	•	•	•	•	•	•	EU Bandel 1998; Lorouet 1998	
<i>Sci. depressa</i> Reuss, 1860 [†]	•	•	•	•	•	•	•	EU Bandel 1998	
<i>Sci. cossmanni</i> Depontaillier, 1881 [†]	•	•	•	•	•	•	•	EU Bandel 1998	
<i>Sci. dohrniana</i> (Dunker, 1861) (<i>Anatomus</i>)	•	•	•	•	•	•	•	IO Thiele 1912; Yaron 1983	
<i>Sci. electilis</i> Montouchet, 1972	•	•	•	•	•	•	•	SA Montouchet 1972	

<i>Sci. elegans</i> d'Orbigny, 1824	EU	cf. Marshall 2002
<i>Sci. eocaenica</i> Bandel, 1998 [†]	EU	Bandel 1998
<i>Sci. evaeensis</i> Bandel, 1998	IP	Bandel 1998
+ <i>M.. unispirata</i> Bandel, 1998	IP	Bandel 1998
<i>Sci. eucharistia</i> Melvill & Standen, 1912	IP	Forcelli 2000
<i>Sci. fairchildi</i> Powell, 1933	SA	Powell 1933
<i>Sci. hoernesii</i> Semper, 1865	NZ	Anistratenko and Starogobatov 1997; cf. Marshall 2002
<i>Sci. josephinae</i> Odhner, 1960	IP	Thiele 1912; Bandel 1998
<i>Sci. jacunda</i> Smith, 1890	NA	Burnay and Rolán 1990
<i>Sci. koeneri</i> Scmpet, 1865	IO	Thiele 1912; Herbert 1986
<i>Sci. laevigata</i> d'Orbigny, 1824	IP	Thiele 1912; Bandel 1998
+? <i>Sci. costata</i> d'Orbigny, 1824	EU	Anistratenko and Starogobatov 1997; cf. Marshall 2002
<i>Sci. lobini</i> (Burnay & Rolán, 1990) (<i>Sinezona</i>)	NA	Burnay and Rolán 1990
<i>Sci. marshalli</i> Bandel, 1998	NZ	Bandel 1998
<i>Sci. manawatawhia</i> Powell, 1937	NZ	Powell 1937
<i>Sci. medioplicata</i> Thiele, 1925	SA	Thiele 1925
<i>Sci. mirifica</i> (A. Adams, 1862) (<i>Anatomus</i>)	NP	Thiele 1912
<i>Sci. morretzei</i> Montouchet, 1972	SA	Montouchet 1972
<i>Sci. ? munieri</i> P. Fischer, 1962	NP	Thiele 1912
<i>Sci. ornata</i> May, 1908	AU	Jansen 1999; D. L. Geiger, unpublished data
<i>Sci. petermannensis</i> Lamy, 1910	AN	Thiele 1912
<i>Sci. prendrevillei</i> Powell, 1933	NZ	Powell 1979; Marshall 2002
+ <i>Sci. stellae</i> Fleming, 1948	(Marshall 2002)	
<i>Sci. pseudoequatoria</i> Kay, 1979	CP	Kay 1979
<i>Sci. redfernii</i> Rolán, 1996	NA	Rolán 1996; Redfern 2001
<i>Sci. reticulata</i> Philippi, 1853	IO	Bouchet and Danrigal 1982; Yaron 1983; Bandel 1998
<i>Sci. richardii</i> Dautzenberg & H. Fischer, 1896	NA	Thiele 1912
<i>Sci. rota</i> Yaron, 1983	IO	Yaron 1983; Herbert 1986; Bandel 1998; D. L. Geiger, unpublished data
<i>Sci. smithi</i> Thiele, 1912	IO	Thiele 1912
<i>Sci. staminea</i> (A. Adams, 1862) (<i>Anatomus</i>)	NP	Thiele 2001; D. L. Geiger, unpublished data

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Appendix 1. (continued)

<i>Sin. moucheti</i> (Vélin, 1877) (<i>Schismope</i>)	•	•	IO	Vélin 1877; Thiele 1912
<i>Sin. pacifica</i> (Oliver, 1915) (<i>Schismope</i>)	•	•	AU	Bandel 1998; Jansen 1999; D. L. Geiger, unpublished data
+ <i>Dai. pacifica</i> Bandel, 1998				(Marshall 2002)
<i>Sin. padangensis</i> (Thiele, 1912) (<i>Schismope</i>)	•	•	IP	Thiele 1912
<i>Sin. paumotensis</i> (Garrett, 1872) (<i>Scissurella</i>)	•	•	CP	Thiele 1912
<i>Sin. plicata</i> (Hedley, 1899) (<i>Schismope</i>)	•	•	IP	Thiele 1912; Bandel 1998; Jansen 1999; Okutani and Hasegawa 2000 (as <i>Sci. coronata</i>); D. L. Geiger, unpublished data
<i>Sin. rimuloides</i> (Carpenter, 1865) (<i>Scissurella</i>)	•	•	NP	McLean 1971, 1989; Finet 1993; Kaiser and Bryce 2001
<i>Sin. semicostata</i> Burnay & Rolán, 1990	•	•	NA	Burnay and Rolán 1990
<i>Sin. zimmeri</i> n. sp.	•	•	CP	This study
<i>Suk. armillatus</i> (Yaron, 1993) (<i>Sinezona</i>)	•	•	IO	Yaron 1993
<i>Suk. atkinsoni</i> (Tenison Woods, 1876) (<i>Scissurella</i>)	•	•	AU	Thiele 1912; Cotton 1959; Bandel 1998 (also as <i>Suk. declinans</i>); Jansen 1999; D. L. Geiger, unpublished data
+ <i>Schis. carinata</i> Watson, 1886 (non Adams, 1862)	•	•	Watson 1886	Watson 1886
<i>Suk. carinatus</i> (A. Adams, 1862) (non Watson, 1886)	•	•	IP	Thiele 1912; Habe 1951; Kuroda et al. 1971; Jansen 1999; Higo et al. 2001;
(<i>Scissurella</i>)			D. L. Geiger, unpublished data	
<i>Suk. (?) dorbigyi</i> (Audouin, 1826) (<i>Scissurella</i>)	•	•	IO	Bouchet and Daanrigal 1982; Yaron 1983
<i>Suk. indonesicus</i> Bandel, 1998	•	•	IP	Bandel 1998
<i>Suk.. hyallensis</i> (Finlay, 1926) (<i>Schismope</i>)	•	•	NZ	Powell 1979; Marshall 1993
<i>Suk. maraisi</i> Herbert, 1986	•	•	IO	Herbert 1986; Bandel 1998
+ <i>Suk. peilei</i> Auct.			IO	Bandel 1998
<i>Suk. mirandus</i> (A. Adams, 1862) (<i>Scissurella</i>)	•	•	NP	Thiele 1912 (<i>nomen dubium</i> ? : see remarks under <i>Sukashirothus</i>)
<i>Suk. pulcher</i> (Pettied, 1884) (<i>Schismope</i>)	•	•	AU	Thiele 1912; Cotton 1959; Jansen 1999; D. L. Geiger, unpublished data
<i>Suk. simplex</i> Bandel, 1998	•	•	IP	Bandel 1998
<i>Suk. tasmanicus</i> (Pettied, 1879) (<i>Schismope</i>)	•	•	AU	Thiele 1912; Bandel 1998
<i>Suk. tricarinatus</i> (Yaron, 1983) (<i>Sinezona</i>)	•	•	IO	Yaron 1983
<i>Sutilizona</i>				
<i>Sut. pterodon</i> Warén and Bouchet, 2001	•	•	NA	Warén and Bouchet 2001

(continued next page)

Appendix 1. (continued)

Species	DR	LM	SEM	PC	R	EA	H	Z	References
<i>Sut. rheeca</i> McLean, 1989	•	•	•	•	•	•	NP		Haszprunar 1989; McLean 1989
<i>Sut. hinnicifae</i> Waren & Bouchet, 2001	•	•	•	•	•	•	NA		Waren and Bouchet 2001
<i>Tennocochlis</i>	•	•	•	•	•	•	NP		Haszprunar 1989; McLean 1989
<i>Tc. euripes</i> McLean, 1989	•	•	•	•	•	•	NP		Haszprunar 1989; McLean 1989
<i>Tennozaga</i>	•	•	•	•	•	•	NP		McLean 1989; Haszprunar 1989
<i>Tz. parilis</i> McLean, 1989	•	•	•	•	•	•	NP		McLean 1989; Haszprunar 1989
<i>Troglononcha</i>	•	•	•	•	•	•	IP		This study
<i>Tr. christinae</i> n. sp.	•	•	•	•	•	•	IP		EU
<i>Tr. marshalli</i> (Lozouet, 1998) [†] (<i>Larocheopsis</i>)	•	•	•	•	•	•	IP		Lozouet 1998
<i>Tr. olashii</i> Kase & Kano, 2002	•	•	•	•	•	•	IP		Kase and Kano 2002
<i>Tr. tessellata</i> Kase & Kano, 2002	•	•	•	•	•	•	NP		Bandel 1998 (as <i>La. miranda</i>); Kase and Kano 2002; D. L. Geiger, unpublished data

DR, Drawings; LM, lightmicrographs; SEM, scanning electron micrographs of shell; PC, protoconch (SEM); R, radula (LM or SEM); EA, external anatomy; H, histiology; Z, zoogeographic province; AN, Antarctic; AU, Australia; CP, central Pacific; EU, Europe; IP, Indo-Pacific; NA, North Atlantic; NP, north Pacific; NZ, New Zealand; IO, Indian Ocean; SA, South Atlantic; TP, Tropical Pacific.

[†]The specimens illustrated by Bandel (1998) from the South China Sea and Satonda, Indonesia, as well as Jansen (1999) from the Northern Territory and south Western Australia as the South African *An. agulhasensis*, actually show the South Japanese *An. turbinata*. The proportion of the aperture to the overall shell size and the size of the shoulder clearly distinguish the two species. The geographic distribution of the two species is also much more plausible than the widespread distribution of *An. agulhasensis* noted by Bandel.

²Synonymy fide McLean (1967). It is unclear whether there really is a single species in the northern hemisphere. SEM data are not available.

³The generic placement of the species is highly tentative because it has never been illustrated and was overlooked in Herbert's (1986) revision of the South African species. Barnard (1963) compared his 'Sci.' *africana* with his 'Sci.' *tabulata*. As the latter is an *Anatoma* s.l., 'Sci.' *africana* is tentatively placed among the *Anatoma* s.l.

⁴Note added in proof. The type material of *Ar. lacuniformis* was recently inspected at The Natural History Museum, London. The specimens are not Scissurellidae and the foramen shown in Watson's illustration is most likely overly stylized shell damage. The true systematic position of these shells awaits further study.

[†]Fossil species.

Appendix 2. Data matrix used for the phylogenetic analysis of Scissurellidae, including three outgroup taxa (*Emarginula*, *Pleurotomaria*, Trochidae)

Characters are described in the main part of the text

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Emarginula</i>	2&6	1	0	2	0	0	A	0	3	0	0	0	0	0	2	C	1	1
Pleurotomariidae	0	0	1	0	0	1	0	0	4	0	0	0	0	0	2	A	1	1
Trochidae	0	0	1	0	0	1	0	0	0	0	0	2	2	B	2	D	1	1
<i>Sat. minuta</i>	0	0	?	1	0	2	0	0	2	0	1	1	1	1	?	?	?	?
<i>Sat. semi</i>	2	0	0	1	1	2	0	0	2	0	1	1	1	1	?	?	?	?
<i>Sci. alito</i>	0	2	0	0	1	2	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. columbiana</i>	4	1	0	0	0	1	1	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. coronata</i>	2	2	0	0	1	2	H	0	2	0	0	1	1	0	0	0	1	1
<i>Sci. cossmanni</i>	4	2	0	0	0	2	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. cyprina</i>	3	0	1	0	0	1	0	0	2	0	0	1	1	0	1	0	1	1
<i>Sci. declinans</i>	3	2	0	0	1	2	0	0	0	3	0	0	1	1	0	1	0	1
<i>Sci. depressa</i>	3	1	0	0	0	1	0	0	0	2	0	0	1	1	0	?	?	?
<i>Sci. depontailieri</i>	3	2	0	0	0	1	0	0	0	2	0	0	1	1	0	?	?	?
<i>Sci. eocaenica</i>	3	2	0	1	0	2	0	0	2	0	0	0	1	1	0	?	?	?
<i>Sci. evensis</i>	3	2	0	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?
<i>Sci. fairchildi</i>	3	0	1	0	1	2	0	0	1	0	0	1	1	0	?	?	?	?
<i>Sci. hoernesi</i>	0	2	0	0	2	0	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. jucunda</i>	4	1	1	0	0	0	J	0	3	0	0	1	1	0	1	0	1	1
<i>Sci. koeneni</i>	4	2	0	0	1	2	0	0	3	0	0	1	1	0	?	?	?	?
<i>Sci. lobini</i>	4	0	0	0	1	0	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. marshalli</i>	3	1	1	0	0	2	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. ornata</i>	4	1	0	0	0	2	0	0	2	0	0	0	1	0	?	?	?	?
<i>Sci. peyerensis</i>	0	1	0	0	0	2	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. pendrevillei</i>	3	0	0	0	1	1	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. referni</i>	3	0	0	0	0	1	0	0	2	0	0	1	1	0	?	?	?	?
<i>Sci. reticulata</i>	3	1	0	0	0	K	0	3	0	0	0	1	1	0	?	?	?	?
<i>Sci. rota</i>	3	2	0	0	0	2	0	0	2	0	0	1	1	0	1	0	1	1

(continued next page)

Appendix 2. (continued)

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Sci. staminea</i>	4	1	0	0	0	0	2	0	0	2	0	0	1	1	0	?	?	?
<i>Sci. sudanica</i>	3	2	0	0	0	0	1&2	0	0	3	0	0	1	1	0	?	?	?
<i>Sin. bandeli</i>	4	1	1	0	0	1	0	0	0	2	0	1	1	0	?	?	?	?
<i>Sin. beddomei</i>	4	1	0	0	1	2	0	0	2	0	1	1	1	0	1	0	1	1
<i>Sin. brevis</i>	4	1	1	0	0	1	0	0	0	2	0	1	1	1	0	1	0	1
<i>Sin. cingulata</i>	4	1	1	0	0	0	0	L	0	2	0	1	1	1	0	1	0	1
<i>Sin. confusa</i>	4	2	0	0	0	1	0	0	0	2	0	1	1	0	?	?	?	?
<i>Sin. crossei</i>	4	1	0	0	0	1	0	0	0	2	0	1	1	0	?	?	?	?
<i>Sin. dolium</i>	4	1	0	0	0	0	M	0	2	0	1	1	1	0	?	?	?	?
<i>Sin. ferriezi</i>	0	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	0	1
<i>Sin. iota</i>	4	0	1	0	0	1	0	0	0	1	0	1	1	0	1	0	1	1
<i>Sin. pacifica</i>	4	1	1	0	0	1	0	0	0	2	0	1	0	1	0	1	0	1
<i>Sin. plicata</i>	2	2	0	0	0	1	0	0	0	2	0	1	1	0	1	0	1	1
<i>Sin. levigata</i>	4	1	1	0	0	0	N	0	3	0	1	2	1	0	?	?	?	?
<i>Sin. semicostata</i>	4	0	0	1	0	0	P	0	2	0	1	1	0	?	?	?	?	?
<i>Suk. atkinsoni</i>	3	2	0	0	0	2	0	0	4	1	1	1	0	0	1	0	1	0
<i>Suk. carinatus</i>	3	1	0	0	0	2	0	0	2	1	1	1	1	0	0	0	1	1
<i>Suk. indonesicus</i>	3	2	0	0	1	2	1	0	2	1	1	1	1	0	?	?	?	?
<i>Suk. maraisi</i>	0	1	0	0	0	2	1	0	2	1	1	1	0	?	?	?	?	?
<i>Suk. pulcher</i>	6	1	0	0	0	2	0	0	3	1	1	1	0	0	0	1	1	0
<i>Suk. simplex</i>	3	2	0	0	0	2	1	0	2	1	1	1	1	0	?	?	?	?
<i>Ar. subantarctica</i>	3	0	0	0	0	0	B	0	0	0	1	2	1	2	1	0	1	1
<i>Ar. pauperaia</i>	4	0	1	0	0	?	?	0	1	0	1	2	1	0	?	?	?	?
<i>Ar. halimimorpha</i>	3	1	1	0	0	0	C	0	2	0	1	2	1	0	?	?	?	?
<i>C. simondsae</i>	3	0	0	0	0	1	0	1	0	1	0	2	2	M	M	1	0	1
<i>I. 'auriform'</i>	4	0	1	2	0	1	1	0	0	0	1	1	1	2	1	1	0	1
<i>I. hyttelionensis</i>	4	0	1	2	0	1	1	0	0	0	1	1	1	2	1	1	0	1
<i>I. rosea</i>	4	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
<i>I. fossilis</i>	4	0	1	2	0	2	0	0	3	0	0	0	1	1	2	1	?	?

Obituary

Richard Kenneth ('Dick') Dell, 1920–2002: obituary, bibliography and a list of his taxa

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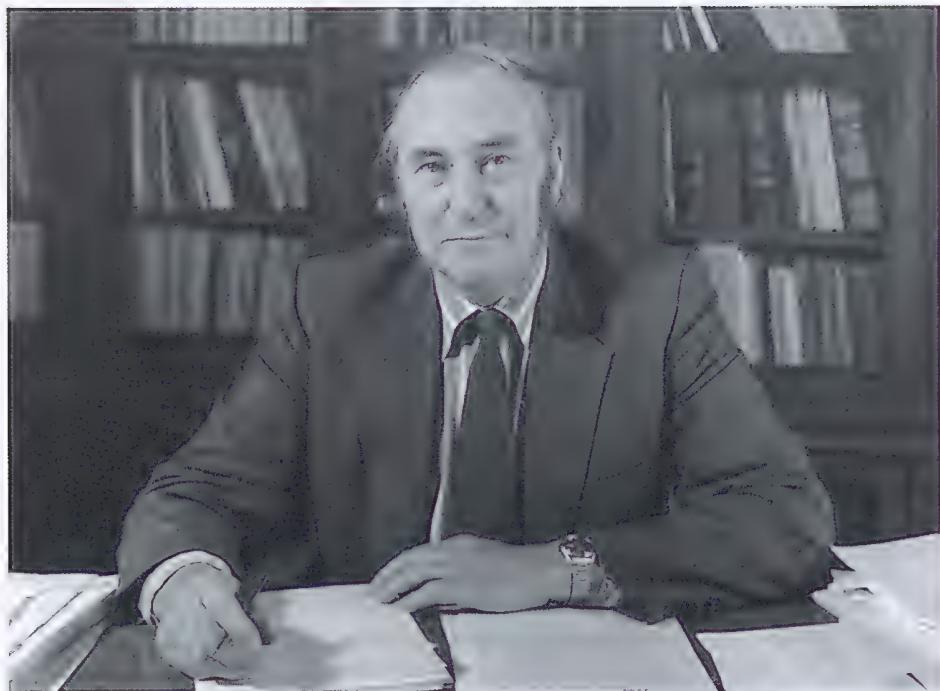
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Obituary

Dr 'Dick' Dell was the last of the immediate past generation of 'giants' of New Zealand malacology. He was born in Auckland on 11 July 1920 and died on 6 March 2002, after a long illness, surrounded by his family, at the Mary Potter Hospice, Wellington. He is survived by his wife, Dame Miriam (née Matthews), whom he married in 1946, and four daughters. He left a legacy of a major museum collection at the Museum of New Zealand Te Papa Tongarewa (formerly the National Museum of New Zealand, the Dominion Museum, and originally the Colonial Museum). He published several major monographs and more than 150 papers on Mollusca, more than 300 new species, and several popular books on shells and crabs. We list here his publications and new taxa, following a brief biography.

As a 12-year-old, Dick started collecting shells from the shores of Waitemata Harbour. With a friend, he started a museum in the back yard of his home. He was one of the early members of Baden Powell's 'boys' club' at the Auckland Museum, later to become the large, still strong Auckland shell club (formally, the Malacology Section, Auckland Institute and Museum). There he met and became life-long friends with that other 'giant' of New Zealand natural history, Charles Fleming. He also worked for Powell in the school holidays, helping curate the Auckland Museum shell collection. He was educated at Mount Albert Grammar School, Auckland University College and Auckland Teachers College, and he would have been a teacher if the war had not intervened. With the war, Dick joined the New Zealand Artillery and served in, among other places, Nissan Island in the Solomon Islands, where he was able to collect (and he later published several papers on the land snails he collected there). He also served in the Middle East and Italy.

After the war, Dick was about to take up teaching when he was offered a job as 'conchologist' at the Dominion Museum, replacing Marjorie Mestayer. He jumped at the offer and went on to a career in malacology. He inherited a relatively small, chaotic, quaintly stored collection of a mere 5000 registered lots, mostly dating from Colonial Museum times. He standardised museum cabinets, tubes and trays, and built the collection up to more than 30 000 lots by the time Winston Ponder replaced him as malacologist in 1967. He thus laid a firm foundation for the future development of this now globally significant collection. Dick was one of the many who returned from the war to a civil life where the struggle to earn a part-time degree was combined with holding down a full-time job and raising a family. He completed an MSc at Victoria University (Wellington) on New Zealand



Richard (Dick) Dell in his office at the National Museum of New Zealand in 1975.

octopus and squid (published as *Dominion Museum Bulletin 16*, 1952), a pioneering effort at a time when few taxa had been collected around New Zealand. Probably Dick's major contribution to knowledge of the New Zealand molluscan fauna was the results of the Chatham Islands 1954 Expedition, the first major oceanographic expedition beyond the shelf edge around New Zealand. This was published in 1956 as 'The archibenthal Mollusca of New Zealand' (Dell 1956c). In this major monograph, Dick provided evidence to explain the long-mysterious depositional environments of New Zealand's richly diverse Cainozoic fossil molluscan fauna: many faunas lived beyond the shelf edge, at 300–400 m depth and more. Here, such treasures as *Parvamussium*, *Euciroa*, *Otukaia*, *Falsilunatia*, *Galeoidea*, *Sassia kampyla*, large turrids, and *Scaphander* were discovered for the first time living around New Zealand, and several of the species collected by HMS '*Challenger*' were re-collected for the first time. This was a great revelation to palaeontologists and we young students alike! It has led on to the detailed knowledge of and huge collections from the bathyal zone of the New Zealand region, held at the Museum of New Zealand Te Papa Tongarewa and the National Institute of Water and Atmospheric Research. This publication also served to earn Dick a DSc, awarded in 1956.

Not long afterwards, Dick started to work on the Oceanographic Institute's Antarctic collections, and both Winston Ponder and Alan Beu well remember highly enjoyable school vacations being paid (!) to sort shells from those samples, mainly from the Ross Sea. Dick worked also on other Antarctic collections and, in 1964, published a major monograph of the Antarctic bivalves, chitons and scaphopods collected by the '*Discovery*' Expedition (A. W. B. Powell having revised the gastropods). In 1961, he became Assistant Director (to Dr Robert Falla) and, in 1966, Director of the then Dominion Museum and had little time

to work on molluscs. However, after his retirement in 1980, he again set to work to write up the Ross Sea molluscs. This study was eventually published as a book, 'Antarctic Mollusca, with Special Reference to the Fauna of the Ross Sea' (Dell 1990c), and is one of only a few synoptic treatments of the Antarctic Mollusca. Along the way, Dick published more than 150 other papers on marine, terrestrial and freshwater molluscs (including fossils), crabs, birds and other groups, as well as several contributions to Antarctic biogeography.

We remember Dick as a very kind, patient man, very helpful and encouraging to everyone. He would go out of his way to identify that one last little snail that defied the literature, providing much satisfaction to the collector and the inspiration for a life of research. In this vein, one of his major contributions to New Zealand malacology was his founding of the Wellington Shell Club in 1955. Early members included schoolboys Winston Ponder and Alan Beu, with Frank Climo and Bruce Marshall joining later. Early meetings were held in Dick's office, with only six to eight people present, but the club soon had to move to the boardroom and continues in strength today. Dick also had a passion to conserve the rich New Zealand fauna and flora and anyone who collected with him will always remember his loud cry of 'Turn the boulder [or log] back over!'.

Dick served an astonishing variety of societies and committees that keep science active and organised in New Zealand. Among others, these included the Historic Places Trust, the Ross Dependency Research Committee, the National Parks and Reserves Authority (his work in which was of particular significance), the NZ Ecological Society, the NZ Marine Sciences Society (President 1963–65), the Art Galleries and Museums Association of NZ (President 1958–59), the Scientific Subcommission of UNESCO, and the Royal Society of New Zealand (including Editor of *The Transactions*, 1964–69, and President, 1977–81). He was awarded a Nuffield Travelling Fellowship in 1959–61 to work on New Zealand molluscs at the British Museum (Natural History). He was elected a Fellow of the Royal Society of New Zealand in 1961 and won the Society's Hamilton Prize in 1955, and the Hector Medal of the Society in 1965. He was also awarded a Galathea Medal by Denmark, a Queen's Service Order in 1981, a Queen's Silver Jubilee Medal, and a New Zealand 1990 Commemoration Medal. We are particularly sad to see him go, as he was a mentor and friend to all three authors, and the last of his great generation of New Zealand biologists and taxonomists, who brought these sciences to the established position they have today. He will long be remembered for this legacy.

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New taxa

MOLLUSCA

abernethyi, *Antiguraleus*. Dell, 1956c: 138.

abernethyi, *Xenophalium (Xenogalea)*. Dell, 1956c: 87.

abruptia, *Linemera*. Dell, 1956c: 66.

aerari, *Diplommatina*. Dell, 1955e: 424.

alacerrima, *Herpetopoma larochei*. Dell, 1956a: 34.

alacris, *Uberella*. Dell, 1956c: 77.

alertae, 'Balcis'. Dell, 1956c: 81.

alertae, *Fax*. Dell, 1956c: 92.

Alertalex. Dell, 1956c: 46; type species (OD) *Alertalex blacki* Dell, 1956 (Trocidae).

allanae, *Obanella*. Dell, 1952d: 89.

altocanalis, *Coluzea*. Dell, 1956a: 50.

altocanalis, *Ringicula*. Dell, 1952c: 82.

ambigua, *Lissotesta*. Dell, 1956c: 53.

anarensis, *Solariella*. Dell, 1972b: 3.

anomalus, *Terefundus*. Dell, 1956c: 115.

antarctica, *Belaturricula*. Dell, 1990a: 228.

antarctica, *Brookula (s. l.)*. Dell, 1990a: 102.

antarctica, *Calliotropis (Solaricida)*. Dell, 1990a: 86.

antarctica, *Murdochella*. Dell, 1990a: 124.

Antarctodomus. Dell, 1972e: 5; type species (OD) *Bathydomus thielei* Powell, 1958 (Buccinidae).

anteaustrale, *Amphidesma (Paphies)*. Dell, 1950b: 32.

aoteana, *Antizafra*. Dell, 1956c: 111.

aotearoa, *Lyonsiella*. Dell, 1995a: 9.

archibenthicola, *Micrelenchus caelatus*. Dell, 1956c: 44.

arcuatis, *Adipicola*. Dell, 1995a: 4.

attenuata, *Mysella*. Dell, 1956a: 33.

auklandica, *Closia?*. Dell, 1950b: 36.

aupouria, *Cuspidaria*. Dell, 1950a: 21.

aupouria, *Opimilda*. Dell, 1956a: 39.

austrobenthalis, *Nucula*. Dell, 1990a: 6.

austrodimorphus, *Allodiscus*. Dell, 1955b: 1137.

axirugosus, *Terefundus*. Dell, 1956c: 115.

badenpowelli, *Leucosyrinx*. Dell, 1990a: 224.

banksi, *Proximitra*. Dell, 1951d: 54.

bathamae, *Baryspira*. Dell, 1956c: 124.
benthicola, *Buccinulum (Evarnula)*. Dell, 1951d: 56.
benthicola, *Austrosarepta*. Dell, 1956c: 15.
benthicola, *Austrotindaria*. Dell, 1956c: 13.
benthicola, *Baryspira novaezelandiae*. Dell, 1956c: 124.
benthicola, *Brookula*. Dell, 1956c: 49.
benthicola, *Falsimargarita*. Dell, 1990a: 97.
benthicola, *Fenestrosyrinx*. Dell, 1956c: 141.
benthicola, *Itia*. Dell, 1962c: 72.
benthicola, *Liracraea odhneri*. Dell, 1956c: 140.
benthicola, *Pachymelon (Palomelon)*. Dell, 1963e: 213.
benthicola, *Penion*. Dell, 1956c: 96.
benthicola, *Scintillona*. Dell, 1956c: 31.
benthicola, *Splendrilla*. Dell, 1956c: 133.
benthicola, *Tasmocrossea*. Dell, 1952e: 105.
benthicola, *Terelimella*. Dell, 1956c: 156.
benthicola, *Venustas*. Dell, 1950c: 47.
benthicola, *Zemitrella*. Dell, 1956c: 110.
benthicolus, *Aeneator (Ellicea)*. Dell, 1963e: 210.
benthicolus, *Bulbus*. Dell, 1990a: 158.

Benthomodiolus. Dell, 1987: 31; type species (OD) *Benthomodiolus lignocola* Dell, 1987 (Mytilidae).
bioperculata, *Kerguelenatica*. Dell, 1990a: 145.
bisculpta, *Chlanidota*. Dell, 1990a: 185.
blacki, *Alertalex*. Dell, 1956c: 46.
blacki, *Ptychodon*. Dell, 1955b: 1142.
bollonsi, *Crosseola*. Dell, 1956a: 36.
bountyensis, *Haurakia*. Dell, 1950a: 24.
brookesi, *Charopa (Pseudogestula) transenna*. Dell, 1954a: 145.
bruuni, *Cardiomya*. Dell, 1956a: 34.
bulloidea, *Cylichna*. Dell, 1956c: 144.
canturiensis, *Fax mirabilis*. Dell, 1951d: 56.
canyonensis, *Antimelatoma*. Dell, 1956c: 142.
capillata, *Philobrya*. Dell, 1964h: 170.
carcellesi, *Bulbus*. Dell, 1990a: 155.
carolus, *Ruapukea*. Dell, 1952a: 417.
caswelli, *Phrixgnathus viridula*. Dell, 1955b: 1145.

Cavellioropa. Dell, 1952d: 93; type species (OD) *Diplomphalus subantialba* Suter, 1890 (Charopidae).
chathamensis, *Icoplax*. Dell, 1960e: 153.
chathamensis, *Leporemax*. Dell, 1956c: 120.
chathamensis, *Liratilia conquisita*. Dell, 1956c: 110.
chathamensis, *Venustas tigris*. Dell, 1950c: 43.

Chathamidia. Dell, 1956c: 118; type species (OD) *Chathamidia expeditionis* Dell, 1956 (Turbinellidae).
chorista, *Cominella (Cominista)*. Dell, 1952c: 77.
circumcincta, *Zemitrella*. Dell, 1962c: 71.
clarificata, *Acharax*. Dell, 1995a: 2.
conjuncta, *Friginatica*. Dell, 1953d: 43.
cookiana, *Crosseola*. Dell, 1952a: 415.
cookiana, *Geminoropa (Cavellioropa)*. Dell, 1952d: 93.
cookiana, *Histioteuthis*. Dell, 1951d: 1.
cookiana, *Lissotestella*. Dell, 1956a: 36.
cookiana, *Mathildona*. Dell, 1956a: 39.
cookiana, *Monodilepas*. Dell, 1953a: 149.
cookinanus, *Aeneator otagoensis*. Dell, 1956c: 99.
coronata, *Comptella*. Dell, 1956c: 117.
corpulentoides, *Odostomia*. Dell, 1956c: 157.
cracens, *Marginella (Gabella)*. Dell, 1956c: 128.
crassilabrum, *Cyamocardium*. Dell, 1964h: 204.

cryptocarinata, *Pleia*. Dell, 1956c: 89.
delectabile, *Euciroa*. Dell, 1956c: 42.
delicatula, *Bathybembix* Dell, 1990a: 88.
dispectata, *Tromina*. Dell, 1990a: 208.
drakei, *Bathybembix*. Dell, 1990a: 88.
eltanini, *Asperiscala*. Dell, 1990a: 123.
eltanini, *Calliotropis* (*Calliotropis*). Dell, 1990a: 85.
eltanini, *Chlanidota*. Dell, 1990a: 184.
eltanini, *Ennucula*. Dell, 1990a: 8.
eltanini, *Falsilunatia*. Dell, 1990a: 152.
eltanini, *Miomelon*. Dell, 1990a: 214.
eltanini, *Otukaia*. Dell, 1990a: 92.
endeavourensis, *Liotella*. Dell, 1990a: 103.
endeavourensis, *Pleurotomella* (*Anomalotomella*). Dell, 1990a: 242.
ergastula, *Marginella* (*Glabella*). Dell, 1953d: 45.
expeditionis, *Asperdaphne*. Dell, 1956c: 137.
expeditionis, *Chathamidia*. Dell, 1956c: 118.
explorata, *Notoacmea*. Dell, 1953d: 42.
falklandica, *Cyamiomactra*. Dell, 1964h: 203.
falklandica, *Epicodakia*. Dell, 1964h: 206.
falklandicum, *Neolepton*. Dell, 1964h: 210.
falklandicum, *Siphonodentalium* (*Pulsellum*). Dell, 1964h: 131.
falklandicus, *Cyclopecten*. Dell, 1964h: 181.
Falsitromina. Dell, 1990a: 175; type species (OD) *Tromina bella* Powell, 1951 (Turridae).
fectoloides, *Allodiscus*. Dell, 1955b: 1139.
fiordlandica, *Maoriconcha*. Dell, 1952b: 64.
fiordlandica, *Ptychodon*. Dell, 1955b: 1143.
fissurata, *Pachymelon* (*Palomelon*). Dell, 1963e: 213.
Flammoconcha. Dell, 1952b: 65; type species (OD) *Helicarion* (*Peloparion*) *cumberi* Powell, 1941
(Charopidae).
flemingi, *Alcithoe*. Dell, 1978b: 167.
flemingi, *Austrotindaria*. Dell, 1956c: 14.
flemingi, *Phrixgnathus*. Dell, 1950d: 57.
flexicostatum, *Buccinulum* (*Evarnula*). Dell, 1956c: 102.
forresti, *Cirsotrema* (*Tioria*). Dell, 1956a: 40.
forsteri, *Phrixgnathus*. Dell, 1952d: 95.
forsteriana, *Venustas*. Dell, 1950c: 51.
foveauxana, *Venustas*. Dell, 1950c: 45.
fusiformis, *Antiguraleus*. Dell, 1956c: 140.
fusuloides, *Marginella* (*Volvarinella*). Dell, 1956c: 128.
gadus, *Ptychodon*. Dell, 1954a: 142.
galatheae, *Austronucula*. Dell, 1956a: 30.
galatheae, *Questimya*. Dell, 1956a: 33.
gardneri, *Palaina*. Dell, 1955e: 424.
georgiana, *Ennucula*. Dell, 1964h: 142.
georgiana, *Falsimargarita*. Dell, 1990a: 95.
georgiana, *Macoma* (*Psammacoma*). Dell, 1964h: 220.
georgiana, *Pseudokellya*. Dell, 1964h: 200.
glaucarena, *Dentalium* (*Antalis*). Dell, 1953d: 48.
hardingae, *Marginella* (*Kogomea*). Dell, 1956c: 126.
haurakiensis, *Alcithoe* (*Leporemax*) *fusus*. Dell, 1956a: 54.
haurakiensis, *Venustas*. Dell, 1950c: 53.
heardensis, *Laevilitorina* (*Corneolitorina*). Dell, 1964a: 285.
heardensis, *Notodiscus hookeri*. Dell, 1964b: 168.
hedleyi, *Pontiothauma*. Dell, 1990a: 244.
herdmani, *Ledella*. Dell, 1953d: 39.
hermata, *Splendrillia*. Dell, 1956c: 134.

hiarara, *Ptychodon monoplax*. Dell, 1954a: 143.
hurupiensis, *Austrotoma*. Dell, 1952c: 79.
hurupiensis, *Cadulus*. Dell, 1952c: 83.
imporcata, *Fenestrosyrinx*. Dell, 1962c: 73.
inexpectata, *Neactaeonina*. Dell, 1956c: 147.
inexpectata, *Pseudokellya*. Dell, 1964h: 202.
innocentia, *Typhlodaphne*. Dell, 1990a: 240.
investigator, *Thestyleda*. Dell, 1952e: 100.
isolata, *Liratilia*. Dell, 1956c: 111.
jacula, *Splendrillia*. Dell, 1956c: 134.
judithae, *Marginella (Glabella)*. Dell, 1956c: 127.
kapuranga, *Splendrillia*. Dell, 1953d: 46.
knoxi, *Teremelon*. Dell, 1956c: 121.
knudseni, *Limopsis*. Dell, 1990a: 23.
kopua, *Poirieria*. Dell, 1956c: 114.
labioflecta, *Laevilitorina (Corneolitorina)*. Dell, 1990a: 110.
lachlani, *Mysella*. Dell, 1952a: 413.
lamyi, *Chlanidota*. Dell, 1990a: 182.
laqueus, *Phrixgnathus*. Dell, 1950d: 55.
latalamina, *Notoplax*. Dell, 1956a: 57.
lateaperta, *Flammulina*. Dell, 1955b: 1140.
lateumbilicata, *Calliotropis (Solaricida)*. Dell, 1990a: 86.
latior, *Estea rufopapicata*. Dell, 1956c: 63.
lawsi, *Planpyrgiscus*. Dell, 1956c: 156.
librata, *Ledella*. Dell, 1952e: 102.
lignocola, *Benthomodiolas*. Dell, 1987: 33.
mackenae, *Liotella*. Dell, 1956c: 50.
macknighti, *Submargarita*. Dell, 1990a: 91.
macphersonae, *Macquariella*. Dell, 1964a: 282.
manukauensis, *Maorisiphander*. Dell, 1950b: 36.
maoria, *Antimargarita*. Dell, 1995a: 11.
maoria, *Halocardia*. Dell, 1978b: 162.
maoria, *Iridoteuthis*. Dell, 1959b: 3.
maoria, *Pholadomya*. Dell, 1963c: 206.
maoria, *Rissopsetia*. Dell, 1956a: 37.
maoria, *Xanthodaphne*. Dell, 1956c: 136.
Maoriconcha. Dell, 1952b: 62; type species (OD) *Maoriconcha oconnori* Dell, 1952 (Charopidae).
Maoricrater. Dell, 1956c: 57; type species (OD) *Notoacmea explorata* Dell, 1953 (Lepetidae).
Maorisiphander. Dell, 1950b: 36; type species (OD) *Maorisiphander manukauensis* Dell, 1950 (Cylichnidae)
maorium, *Parvamussium*. Dell, 1956c: 20.
marwicki, *Lucinoma*. Dell, 1953d: 39.
marwicki, *Waipaoa*. Dell, 1956c: 112.
matai, *Lironoba*. Dell, 1952a: 416.
maui, *Balcis*. Dell, 1952e: 105.
mawsoni, *Carditella*. Dell, 1972b: 3.
mendica, *Cuna*. Dell, 1952e: 103.
merelina, *Nobolira*. Dell, 1956c: 65.
meridiana, *Zeminolia*. Dell, 1953d: 42.
mernoo, *Condylocardia*. Dell, 1952a: 412.
mestayerae, *Cyclopecten*. Dell, 1956c: 24.
microsculpta, *Poromya*. Dell, 1995a: 10.
microstriatum, *Sinuber*. Dell, 1990a: 161.
miriamae, *Benthindsia*. Dell, 1967: 312.
miriamae, *Scaphander*. Dell, 1952c: 80.
morelandi, *Cuspidaria*. Dell, 1956c: 39.
morioria, *Cuspidaria*. Dell, 1956c: 40.

morioria, *Mysella*. Dell, 1952a: 414.
morioria, *Sacella hedleyi*. Dell, 1956c: 12.
multispiralis, *Aforia*. Dell, 1990a: 231.
multispiralis, *Belatutricula turrita*. Dell, 1990a: 228.
multistriatus, *Antiguraleus*. Dell, 1956c: 139.
neozelanica, *Ectorisma*. Dell, 1956c: 43.
neozelanica, *Enoplateuthis*. Dell, 1959b: 6.
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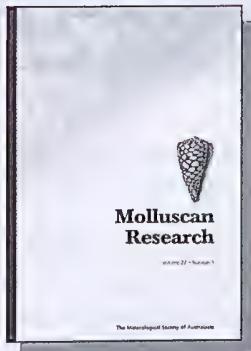
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Julian Cribb and Tjempaka Sari Hartomo

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